A DISSERTATION FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

Species Diversity and Distribution Patterns of Woody Plants in Adaba-Dodola Afromontane Forest, Oromia, Ethiopia

에티오피아 오로미아 아다바-도돌라 Afromontane 숲 목본 식물의 종 다양성과 분포 양상

BY

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DEPARTMENT OF FOREST SCIENCES

GRADUATE SCHOOL

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ABSTRACT

Adaba-Dodola Afromontane forest is one of the biodiversity priority areas of Ethiopia. Nevertheless, this forest is among the most degraded forests in Ethiopian Afromontane forests with remnant fragmented forest patches. Mitigation and restoration of the disturbed forests are taken as priority task for biodiversity conservation and maintaining ecosystem functions. To generate relevant information that helps for maintaining the remaining forest, this study was aimed to explore how the forest species composition, distribution pattern, richness, diversity, structure and regeneration varied with the environment and anthropogenic influences and to evaluate the relative importance of these explanatory variables at different elevation zones.

Three forest sites were considered for the study. 90 plots (20 m × 20 m) were sampled along elevational gradients from two transects of about 1 km apart from all sites. Soil seed bank germination test was performed in greenhouse for six months. Two multivariate analysis models, Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA) models, were performed to examine the relationships between vegetation patterns and explanatory variables. Species diversity indices were used to analyze the pattern of species diversity, richness and evenness. The CCA/ RDA in CANOCO and stepwise multiple regression models were used for variation partitioning among explanatory variables. Analysis of variance (ANOVA) was used for means separation among the significant response variables.

Species-environment ordination computed by CCA/RDA indicated that the variations in woody plant communities were explained by environmental and disturbance factors. The environmental and anthropogenic disturbance data sets in the entire vegetation, respectively explained 19 % ($p = 0.005$) and 26 % ($p = 0.005$) of the total variations (TVE) in species diversity and 37 % ($p = 0.045$) and 24 % ($p < 0.045$) of the total variation in species richness. The species richness ($R^2 = 0.36$; $p < 0.006$) and diversity ($R^2 = 0.47$; $p < 0.001$) showed a pronounced shift at mid elevation gradient exhibiting a hump shape pattern. The mid elevation maximum richness and

diversity patterns were presumed to be emanated from many factors as indicated by multivariate models and analysis of variance. One of the main reasons might be the less anthropogenic activities such as cutting, grazing, settlement and canopy openness as compared to the low and high elevation sites. The less anthropogenic disturbances in the mid elevation in turn were attributed to the high topographic roughness (steep and undulating slope) that might have limited the ease accessibility of the forest for anthropogenic activities. Moreover, the middle elevation is the transitional zone between the lower and the upper zones that might have enabled the site to share some climatic conditions from both elevation zones. According to our climate data, this site was supposed to have moderate climatic conditions (1059 mm mean annual rainfall and 11 ^{o}C mean annual temperature) that might be favorable to sustain more number of species to coexist.

At low elevation, the variance partitioning models indicated that pure anthropogenic factor exerted significant (p <0.005) effect on the species diversity while pure environmental factor did not have significant effect. Cutting disturbance had the most pronounced effect on species diversity at low elevations. However, at the upper end of elevation, the multivariate model analysis indicated that only pure environment had significant influence on the decline of species diversity implying that decline of diversity at the upper end elevation zone was mainly attributed to environmental factors rather than the anthropogenic disturbances. The cool temperature at high elevation (1.7 ^{o}C mean annual minimum temperature) might have accounted for the decline of species richness and diversity by slowing the growth and regeneration rate of plants.

In the soil seed bank, the largest variation in species diversity was explained by cutting (R^2adj =10.8 %; p = 0.038) followed by soil pH (R^2adj = 5.1%; p= 0.029) and aspect (R^2adj = 5.0%; p = 0.014). Jaccard coefficient of similarity showed that there was 73% of dissimilarity between standing vegetation and soil seed bank. The poor species correspondence might be emanated from many reasons. It could be due short-lived seed bank as a result of lack of dormancy mechanisms to persist in the soil,

or due to endocarp dormancy (e.g. *Juniperus procera* and *Olea europaea* species*)* that prevented early germination, or high seed predation by animals (insects) due to fleshy nature of seeds that attract predators (e.g. *Juniperus procera, Ekebergia carpesis* and *Podocarpus falcatus* seeds) or poor viability due to soil borne fungal diseases attacks (e.g. *Podocarpus falcatus;* recent study of seed viability in *Podocarpus falcatus* showed 2.1% viability). Generally, based on soil seed bank evaluation, about 68 % of the woody species of the above ground vegetation was not represented in the seed bank. Based on the regeneration analysis, about 41.27 % of the total species was not regenerating at all, 25.40% species had fair regeneration and 9.52 % had poor regeneration status in Adaba-Dodola Afromontane forest. Moreover, the ecological dominance analysis also revealed that about 81% of the total woody species require immediate conservation priority.

The important findings of the present study were that the joint effect of anthropogenic disturbances and environmental factors had been demonstrated to be a likely mechanism shaping the overall elevational pattern of species distribution, richness and diversity both in aboveground vegetation and soil seed bank. Effect of disturbance, especially cutting was found to be the main factor for the decline of species diversity at low elevations while that of the upper end elevation zone was mainly related to environmental factors rather than the disturbance activities. This implied that the observed patterns of vegetation were not attributed to a single universal explanation but rather to a combination of environmental and anthropogenic factors. Thus, it is highly important to take anthropogenic effects into account when describing ecological processes along elevational gradients.

As a general conclusion, depending only on natural regeneration might not be an effective strategy for restoration of the degraded Adaba-Dodola Afromontane forest implying that enrichment planting with adaptable seedlings is required for successful vegetation restoration, especially for species having low importance value index and poor regeneration status. The forest restoration or conservation efforts need to focus both on maintaining the quantity as well as the quality (species composition) of species

to diversify the species-poor sites. Mitigation of grazing and harvesting disturbances should be considered as one of the main measures that need to be taken into account in forest conservation planning in the study site.

Keywords: Natural regeneration, elevation gradient, disturbance, seed bank, variance partitioning

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ACRONYMS

ANOVA	Analysis of variance
BA	Basal area
BD	Bulk density
CC	Canopy cover
CCA	Canonical correspondence analysis
CO	Canopy openness
DBH	Diameter at breast height
DCA	Detrended correspondence analysis
EDRI	Ethiopian Development Research Institute
EIB	Ethiopia Institute of Biodiversity
IUFRO	International union of forest research organization
GLM	General linear model
GTZ	Germen Agency for Technical cooperation
ISA	Indicator species analysis
IVI	Importance value index
MoFED	Ministry of Finance and Economic Development
NFPA	National forest priority area
PCA	Principal component analysis
RBA	Relative basal area
RD	Relative density
RDA	Redundancy analysis
RF	Relative frequency
SD	Standard deviation

SSB	Soil seed bank
TVE	Total variance explained
V/M	Variance mean ratio
VIF	Variance inflation factor

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1. INTRODUCTION

Tropical Afromontane forests are one of the most species-rich ecosystems on earth (Bussmann, 2004; Mutke & Barthlott, 2005). Afromontane forests mostly occur in the high mountain regions (Friis, 1992; Friis and Sebsebe, 2001; Friis *et al.,* 2010). These forests are internationally recognized as the Eastern Afromontane Biodiversity Hotspot (Mittermeier *et al*., 2004). Ethiopian highland forests are parts of the Eastern Afromontane Biodiversity Hotspots (Mittermeier *et al*., 2004). According to BirdLife International (2012), Ethiopia consists about 40 percent of the Eastern Afromontane biodiversity hotspot. Ethiopian Afromontane biodiversity hotspots harbor an estimated 5200 plant species of which at least 200 are endemic (BirdLife International, 2012). Adaba-Dodola Afromontane forest has been set as one of the primary biodiversity priority areas in Ethiopia.

Despite their high importance as a biodiversity hotspot, the Ethiopian Afromontane forests are one of the most degraded forests and continuously shrinking mainly due to anthropogenic pressures (Feyera *et al*., 2005; Dereje *et al*., 2008). Human population pressure coupled with the suitability of Afromontane forests for agricultural uses made these forests to be under severe land-use pressure, which ultimately led to several fragmentations (Rodrigues *et al*., 2004; Burgess *et al*., 2007; Cordeiro *et al*., 2007). To conserve and maintain the remained fragmented forests, understanding the environmental and anthropogenic factors involved in driving the loss of biodiversity are highly important. In this regard, investigation of the spatial pattern of species diversity and composition, and their driving factors is vital step to develop efficient conservation strategies (Haila & Margules, 1996; Ferrier, 2002; Dudley and Parish, 2006; Fjeldsa, 2007).

One of the most widely reported changes of vegetation patterns for tropical forests was due to variation in species distribution and richness along environmental gradients, especially, elevational gradient (Oliveira and Fontes, 2000). An elevation is one of the important factors shaping the floristic composition, richness and diversity in the mountain regions (Kessler, 2001). Elevation is a surrogate for several covarying environmental gradients (Rahbek, 2005) such as temperature, precipitation and solar radiation (Leathwick *et al.*, 1998; Larcher, 2003). Ethiopia has a very wide elevation range from 116 meter below sea level to over 4000 meters above sea level. This is one of the main reasons for a major role of elevation for plant species diversity in Ethiopia (Woldu *et al*., 1989; Friis, 1992; Gole *et al.,* 2008; Friis *et al*., 2010). Hence, variations in topography, solar radiation, geology and soils contribute strongly to small to large scale scale differences in plant distribution, diversity, richness and species turnover patterns (Allen *et al*., 1991). Detecting the changes in plant species richness and diversity along elevational gradients is one of the most challenges for ecologists (Va´zquez and Givnish, 1998; Hemp, 2006; Martin *et al.,* 2007; Richter, 2008). It is unlikely that studies on species richness and diversity along elevational gradients have found a realistic result for all locations due to the fact that species distributions and richness can also be influenced by other factors such as anthropogenic disturbances (Connell, 1978; Va´zquez and Givnish, 1998), edaphic factors and soil seed bank status (Demel, 1997; 1998).

Anthropogenic influences are also equally important in changing plant distribution and diversity patterns in Ethiopia. Human-induced disturbances such as conversion of forestland to cultivation fields, overgrazing, selective logging and settlement encroachments are generally considered to be among the major causes for habitat alterations (Chown, 2010). In most cases, anthropogenic impacts have seldom

been considered as a potential explanation of elevational patterns of species richness and diversity (Carpenter, 2005; Marini *et al.*, 2009). However, it was recognized in ecological theory that the environmental heterogeneity due to anthropogenic effect is important in controlling biodiversity (Huston, 1994). Hence, the omission of potentially important components of human impact on tree species change might influence understanding of the real mechanisms underlying the observed species–elevation relationship (Marini *et al.*, 2011).

Currently, the focus of vegetation ecologists become on investigations of the factors that affect species distributions and community composition (Motzkin *et al*., 1999) and correlation of vegetation with environmental factors (Clark and Mann, 1999). Many researchers (Colwell *et al*., 2004; Knollová *et al*., 2005) underlined those investigations on vegetation composition, distribution patterns and factors that account for plant distribution, composition and diversity patterns are important input for conservation planning. However, presently, floristic inventories and information on Afromontane forest distribution patterns and regeneration status are at the infant stage in Ethiopia in general and in the study area in particular. Such information is relatively well documented in Kenya and Tanzania (Newmark, 2002; Burgess *et al*., 2007) Afromontane forests. The Ethiopian montane forests have been described mainly based on qualitative field observations (Friis, 1986; 1992; Friis & Demissew, 2001), where only very few quantitative assessments exist (Senbeta *et al*., 2005). Management plans aiming to reconcile forest use and conservation in this forest require data on the floristic diversity patterns, regeneration status and their driving factors. However, there has been no adequate data on the impact of environmental and disturbance variables on plant distribution, diversity, richness and regeneration patterns in Adaba-Dodola Afromontane forest. Therefore, it is high time to investigate

patterns of species distribution, diversity, richness and regeneration and the relative importance of environmental and anthropogenic factors affecting them. The duly resulting information would be essential for developing effective and efficient conservation and restoration plans. Partitioning of variations associated with environmental and disturbance components helps detect mechanisms underlying for community composition, diversity and richness (Legendre *et al*., 2005).

With this background information, this study was hypothesized that there are distinctive patterns of species distribution, composition, richness and diversity along the course of elevation gradients in Adaba–Dodola Afromontane forest; the patterns of community changes were associated with the underlying effects of environmental and anthropogenic factors; there is low similarity between aboveground and soil seed bank vegetation; there is low regeneration ability of Adaba-Dodola Afromontane forests.

With these hypotheses, the study was designed to answer the following questions: What are the main patterns of species distribution, composition, richness and diversity (alpha, beta, and gamma) in Adaba–Dodola Afromontane forest? Do clustered communities along the elevational zone exhibit compositional similarity? What are the principal environmental and anthropogenic factors explaining the variations in vegetation attributes in different clustered communities? What is the relative importance of environmental and anthropogenic variables in determining the variations in forest response attributes? What is the regeneration status of woody plant species in Adaba-Dodola Afromontane forest? Do standing vegetation and soil seed bank flora exhibit similarity pattern? Can the soil seedbanks be considered as a potential source for natural regeneration of the degraded Adaba-Dodola Afromontane

forest; or do they need “passive” (i.e., natural) restoration or “active” (i.e., artificial) restoration strategy?

The general objective of the present study was designed to examine the patterns of species distribution pattern, composition, diversity, richness and natural regeneration in relation to anthropogenic and environmental factors. The specific objectives were: to determine the species distribution, composition, richness, diversity, forest structure and natural regeneration potential of Adaba-Dodola Afromontane forest; to relate the variations of these response variables to environmental and anthropogenic disturbance factors; to partition the variations explained by environmental and anthropogenic factors in species composition, richness and diversity; to determine and suggest the appropriate restoration strategy (active or passive restoration strategy) for the degraded Adaba-Dodola Afromontane forest.

2. LITERATURE REVIEW

2.1. Vegetation classification and ordination

The community classification approaches include physiognomic approach, dominance types, Braun-Blanquet associated approach and numerical approach (Van der Maarel, 1975). Since the community ecologists require to evaluate the effect of multiple environmental factors for many species simultaneously, they employ several multivariate approaches to study the complex nature of plant communities (Gauch and Whittaker, 1972; Gauch, 1982). The functional characteristics of vegetation variables result from the interaction between the properties of the plant species they contain and the environment in which they occur. The hierarchical, polythetic and divisive techniques are frequently employed to analyze vegetation data (Kent and Coker, 1992; Hill, 1994).

Many studies pointed out that among the multivariate approaches, classification is one of the primary methods. Therefore, the method to be used is determined based on the ecological questions to be answered (Gauch and Whittaker, 1972; Gauch, 1982). Classification is the placement of species and/or sample units into groups for the purpose of grouping individual stands into categories. It represents stands which are closely similar with one another, which is separated from other classes that also consists of similar stands (Greig-Smith, 1979). In other words, similar samples are categorized as the same group. The members of each category have in common a characteristic of attributes, which serve to set them different from members of another category (Anderson, 1965). Classification is often useful when assigning names or mapping ecological communities are required.

Ordination is a technique used to order a group of objects along a given gradient (Kent and Coker, 1992). In contrast to classification (i.e., whose objective is to combine similar samples in the same category), the objective of ordination is to show the differences between sample rather than similarities which helps arrange the samples in the form of linear or multi-dimensional relationships with their environment (Kumar, 1981). The usual purpose of ordination in ecological study is to predict the about the relationship existing among the species composition and the underlying environmental factors (Digby and Kempton, 1996). According to same authors, ordination summarizes the patterns of species along environmental gradients by reducing the data into a single graph so that similar species or samples are close together. Digby and Kempton (1987) provided a detail of Direct Gradient Analysis, Detrended Correspondence Analysis (DCA), Principal components analysis (PCA), Canonical Correspondence Analysis (CCA) and many other different ordination approaches. Vegetation classification attempts to identify discrete, repeatable classes of relatively homogenous vegetation communities or association about which reliable statements can be made.

There are a large number of contrasting algorithms available for the classification of samples clustering strategies may be classified according to whether they are hierarchical or non-hierarchical, divisive or agglomerative and polythetic or monothetic (Lambert and William, 1966; Gauch and Whittaker, 1981). If the only requirement in a clustering application is that a given number of clusters be formed (but not related to one another), non-hierarchical may be best (Gauch and Whittaker, 1981).

Divisive methods have an advantage over agglomerative ones in that they use all available information at the initial stage and are less likely to be irrevocably led

astray by chance; the computations are much quicker, since they do not usually continue to the point at which individual classes are recognized as classes (Pielou, 1984). Association analysis was an important early monothetic technique but had an undesirable high rate of misclassification (William and Lambert, 1959; Orloci, 1967).

Polythetic techniques partition on the basis of more than one (usually all) species, such techniques use the data as fully as possible it has the obvious advantage over monothetic techniques in that it can be made to take account of as many properties of the vegetation as we wish to measure or record (Noy-Meyir, 1973; Pielou, 1984). On theoretical grounds, divisive polythetic procedures are superior to both divisive monothetic and agglomerative procedures because a maximum amount of information is used at the major (first) division of hierarchy (Pielou, 1984; Goldsmith *et al*., 1986). Cluster analysis is the general term applied to many techniques used to build classification. The concept of classification in ecological works aims at grouping individual stands or species in to homogenous categories based on their similarity with one another. The stands those are similar with one another form one class, which is separated from other such classes that also consists of similar stands (Digdy and Kempton, 1996). Clustering analysis provides a useful summary when complemented by an ordination (Digby and Kempton, 1996).

2.2. Diversity indices (Alpha, beta and gamma)

The plant community are described by the analyses of species diversity, evenness and similarity (Whittaker, 1975). Diversity index is a mathematical measure of species diversity in a community. Diversity indices provide more information about community composition than simply the number of species present (i.e., species richness); they also take the relative abundances of different species into account (Kent

and Coker, 1992). Diversity and equitability of species are used to interpret the comparative variations between and within the community and help to explain the underlying reasons for such a difference. Generally, the diversity and evenness of a community is calculated using Shannon diversity index (*H*) since it characterizes species diversity in a community and accounting both for abundance and evenness of the species present. Shannon diversity index varies between 1.5 and 3.5 and rarely exceeds 4.5 **(**Magurran, 1988; Kent and Coker, 1992).

Whittaker (1975) expresses the evenness concept as equitability and its base is on the fact that most communities of plant and animals contain a few dominant species and many species that are relatively uncommon. Therefore, evenness measure attempts to quantify this unique representation against a hypothetical community in which all species are equally common such that all species have equal abundances in the community, and hence, evenness is maximal. Examining the degree of association between species and the level of similarity between quadrats or samples is one of the simplest means of analyzing floristic vegetation data and the degree to which the species composition of quadrats or sample matches is alike what is measured with similarity indices (Sorensen's Similarity Index). Its coefficient values ranges from 0 (complete dissimilarity) to 1 (total similarity) (Kent and Coker, 1992).

Alpha (α) and gamma (γ) diversity are considered as diversity inventory, and they have the share same characteristics in common but distinguished only by scale (Jurasinski *et al*., 2009). Alpha diversity is just the diversity of each site (local species pool) while gamma diversity is the diversity of the entire landscape (regional species pool). Beta (β) diversity is describes the changes in species composition between communities (Meynard *et al*., 2011; Sfenthourakis and Panitsa, 2012). The pattern of

species distribution and conservation mechanisms of species diversity along environmental gradients have been core topics in ecological research (Wang, 2009).

Understanding the pattern of species distribution and diversity is essential to develop strategies for conservation under variable environments. Decision on whether a single large or several small areas are appropriate for biodiversity conservation depends on the dominant type of diversity present (Patterson and Atmar, 1986). For example, a high β species diversity within a community type may theoretically imply that the community occupies a heterogeneous environment that implies the use of the 'several small' strategy will be superior to the "single large" strategy in reserve design for species diversity conservation (Wiersma and Urban, 2005).

2.3. Forest regeneration

Study on forest regeneration is an important aspect of predicting forest ecosystem dynamics and restoration potential of degraded forestlands. Sustainable forest restoration is possible only under the availability adequate information on the regeneration dynamics and the possible influential agents. The variations in forest regeneration can be revealed both through differences in their constituent species and the environmental variables in which they grow (Demel, 1997a; Denslow, 1987). Trees can regenerate from many sources such as from seed rain, soil seed bank (dormant seeds in the soil), seedling bank (established, suppressed seedlings in the understory), and coppice (root/shoot sprouts of damaged individuals) (Demel, 1997b; Demel and Granstrom, 1995; Garwood, 1989; Getachew *et al*., 2002).

If the species have continuous regeneration, they reveal the reverse J shape curve distribution pattern of species, which is an indicator of healthy/good

regeneration (Harper, 1977; Demel, 1997a). But such population structures are usually found in natural forests where external disturbances are limited (Demel, 1997a; Feyera, 2006; Getachew *et al*., 2002). According to Bazzaz, (1991), seedling densities in forest understories are dynamic and rates may vary depending on the habitat they grow, for instance the gap and shade environments. Augspurger (1984) and Janzen (1971) also noted that the abiotic and biotic stresses such as light, drought, herbivory, disease or competition determine the rates of regeneration.

Thus, regeneration studies have significant implications on the management, conservation and restoration of degraded natural forests. The Afro-montane forests in Ethiopia, are among the most threatened ecosystems in the country due to conversion to agriculture, commercial logging and loss of biodiversity. Several forests and forest tree species in the country have shown decline in their population structure and regeneration due to past and present disturbances, conversion and management. Disturbances such as intensive removal of trees for timber, construction, and forest grazing have placed significant pressure on forest regeneration (Getachew *et al*., 2002).

2.4. Soil seed bank

Soil seed banks are the aggregations of germinable seeds in the soil potentially capable of replacing adult plants (Baker, 1989; Thompson and Grime, 1979). Most of the seeds in the seed bank come from the nearby parent plants, while the remaining seeds are contributed by plant communities a long distance away from the parent plants (Solomon, 2011). Many plant species have the capacity to produce seeds that remain dormant in the soil for several years to several decades. The capacity to perform persistent seed bank allows species to survive episodes of disturbance and destruction (Thompson, 2000). The same author stated that many species have this capacity and

many do not. Seed persistence, the carry-over of viable seeds in the soil for multiple years, can cushion the effect of local extinction of genotypes in the non-dormant portion of the population, and act to maintain genetic variation during periods when seedlings do not survive to become reproductive adults. Seed banks can also mitigate a population from extinction and preserve the representation of a plant species within a community (Kalisz, 1991) by replacing adult plants (Baker, 1989; Leck *et al*., 1989). They can play a critical role in vegetation maintenance, succession, ecosystem restoration and conservation of genetic variability (Harper 1977; Hills & Morris, 1992; Leck *et al*., 1989; McGraw *et al*., 1991).

However, the potential in using SSB to assist post-disturbance succession management heavily depends on the nature and degree of disturbance inflicted on a site (Granström, 1988). It is very important to understand the potential effects of different disturbances, especially deforestation and subsequent cultivation, on the composition of SSB as these could be a potential threat to biodiversity. An understanding of the functions of SSB requires not just knowledge of the number of seeds present at one time but also knowledge of SSB dynamics (Fenner, 1985). According to Major and Pyott (1966) the inventory of floristic diversity at a site should include the species in the soil seed bank. Several studies indicate that there is little similarity between standing vegetation and the soil seed bank (Bossuyt and Honnay, 2008; Ma *et al*., 2010). Therefore, information about species present in the seed bank and those missing is needed to judge the potential of soil seed bank in restoring the disturbed forestlands.

Although the seed bank is an important element in restoring the fragmented Afromontane forest ecosystems, little is documented on the diversity of the soil seed bank and its relations to the above-ground vegetation in Afromontane forests

particularly in Ethiopia. Such information is crucial for developing programs for conservation and habitat restoration in the remnant Afromontane of Adaba-Dodola which has been severely degraded mainly due to tree lopping, overgrazing and agricultural expansion. The alarmingly increase of forest destruction in Ethiopia necessitated prioritizing forestlands for conservation of the remaining forests. Hence, Adaba–Dodola forest is one of the National Forest Priority Areas (NFPA) for conservation. In this regard, artificial restoration of degraded forestland is cost and labor intensive. Rather, use of soil seed bank in vegetation succession management is acknowledged as it is a low cost restoration technique particularly in economically poor countries like Ethiopia. However, the knowledge on the soil seed bank restoration potential and its relation with the above-ground vegetation in this habitat is very limited.

2.5. Forest degradation in Ethiopia: An overview

Degradation of forest in Ethiopia started since a long century and the intensity varied from space to place. There was a cyclic deforestation and revegetation in the northern part of Ethiopia over the past three millennia while deforestation in the southern part of the country is a relatively recent activity (Darbyshire *et al.*, 2003; Nyssen *et al*., 2004; Dessie, 2007). Darbyshire *et al*. (2003) and Nyssen *et al*. (2004) explained the reason for spatial variation of deforestation is due to population growth, agricultural expansion, urbanization and trade. According to Dessie (2007), in the southern part, deforestation has been increased since the 1950s with a rate of from 140 000–200 000 ha per year (FAO, 2010). The recent report by FAO (2010) indicate that the present remaining forest cover is only about 12.3 million ha of forest.

The dependence of community on agriculture biomass energy are the two most direct drivers of the deforestation in Ethiopia (Reusing, 1998; EDRI, 2010). Land grabbing is also considered as a new threat for the forests of Ethiopia in the present times where large scale leases are given to foreign and local investors especially for production of export crops.

The forest management based public participation in Ethiopia dates back to AD 14th and 15th centuries in three main phases: deforestation phase, substitution phase (use of alternative materials such as dung and crop residue for energy and stone for construction), and restoration phase (Eshetu and Högberg, 2000). Currently, Ethiopia entered a program of forest restoration where large degraded areas are being rehabilitated through mass mobilization and community based forest management programs, but still deforestation has not been abated. According to Tadesse (2007), the remaining forests in the southern region are prone to deforestation. Due to the rehabilitation efforts during the past three decades, most northern highlands of Ethiopia now have more trees and woody biomass than 100 years ago (Ritler, 1997; Jagger *et al*., 2005).

2.6. Patterns of floristic composition and diversity in Ethiopia

Ethiopia is a country of great geographical diversity with high and rugged mountains, flat-topped plateaus and deep gorges, incised river valleys and rolling plains. The Great African Rift Valley runs from north to south bisecting the plateau, and in conjunction with the surrounding lowlands; this feature isolates and separates the plateau from other parts of the continent. The varied topography, the rift valley and the surrounding lowlands have given the country a wide spectrum of habitants and climatic conditions.

The country has a very diverse climatic conditions varying from hot and dry desert in the lowland areas, part of which are as deep as 116 m below sea level, to cold and humid alpine habitats in highlands, which rises to over 4000 masl. Such diverse climatic conditions and habitats contributed to the presence of high species diversity in plants and animals, making Ethiopia one of the top 25 richest countries of the world in biodiversity (Demel, 1999). The potential distribution of a community can be predicted based on meteorological and geological characteristics. At relatively low temperature and high rainfall distribution, evergreen shrubs, herbs and grasses are dominant, while deciduous and spiny shrubs are dominant and grasses are less abundant at low temperature and rainfall distribution (Getachew, 2005). In Ethiopia, topographic features act on local vegetation largely through climate or edaphic features. Similarly, Riley and Young (1966) and Avila (1992) agree on the fact that strong topographical relief tend to produce more marked local climate. Altogether climatic variation become more and more extreme and rapid with increasing altitude, such local climate would not take place if it were not for the topography (Hedberg, 1964).

3. MATERIALS AND METHODS

3.1. Study area description

3.1.1. Location

The study was conducted in Adaba-Dodola Afromontane forest situated between latitude 6º 48’ and 6º 57’ N and longitude 39º 10’ and 39º 26’ E at an elevation range of 2565-3400 m. Geographically, it is located in Adaba and Dodola districts, West Arsi zone of the Oromia Regional State, South eastern Ethiopia (Figure 1). Adaba-Dodola forest is located in the Bale Mountains at a distance of 320 km from Addis Ababa towards the southeast. It is part of the East African Afromontane Biodiversity Hot Spot forest and thus considered as one of the National Forest Priority Areas of the country. Subsistence agriculture and animal husbandry are the main activities in and outside of the forest delineation area.

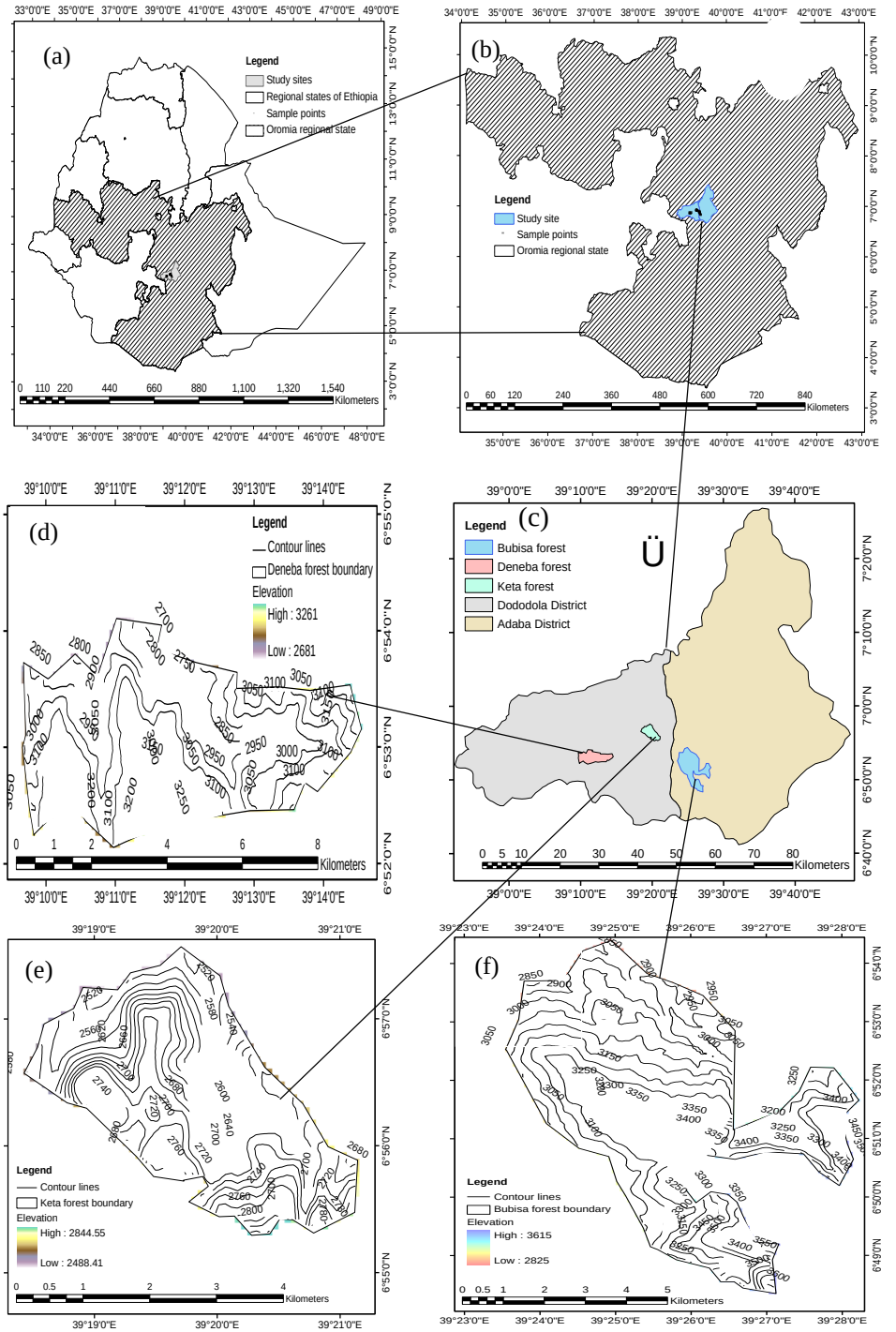


Figure 1. Map of the study area (a) Ethiopia (b) Oromia region (c) Adaba-Dodola district (d) Deneba forest site (e) Keta forest site (f) Bubisa forest site

3.1.2. Climatic conditions

Climate variables, temperature and precipitation, were extracted from the global Worldclim database for the period of 1970-2000 (Fick and Hijmans, 2017; http://www. worldclim.org/version2). The diagram in Figure 2 displays monthly and annual averages for temperature and precipitation over a year in three sites of Adaba–Dodola forests. The meteorological data showed that the Adaba-Dodola forest had a bimodal rainfall pattern in all the three sites. The mean annual temperature of the lower elevation study site was 13.77^{o}C, and the mean minimum and maximum were 4.11 ^{o}C and 21.6 ^{o}C, respectively. The lower elevation area had the mean annual rainfall of 917 mm. This site obtains the main rainfall between March and April and between July and September. The months of November to January were dry periods in low elevation (Table 1 & Figure 2a). The mean annual temperature of the middle elevation study site was about 11.43^{o}C with mean minimum of 2.96 ^{o}C and mean maximum of 18.96 ^{o}C. Annual mean rainfall of 1059 mm was recorded in the middle elevation. The mean annual temperature of the upper elevation study site was about 10.61^{o}C, ranging from mean minimum of 1.7 ^{o}C to mean maximum of 18.15 ^{o}C. The mean annual rainfall record was 1089 mm. The distribution patterns of rainfall across months in the middle and high elevation sites were similar. The peak rainfall was recorded in the months of April and May and July to October both in middle and high elevations (Table 1 and Figure 2b & c). Months of November, December and January receive low rainfall showers. There was no dry season observed in the middle and upper elevation areas of the study site unlike the low elevation.

The mean temperature in Adaba-Dodola forest was observed to decrease with elevation, i.e., from 13.77 ^{o}C at 2678 m to 11.43 ^{o}C at 2942 m and from11.43 ^{o}C at 2942 m to 10.61^{o}C at 3232 m. According to the Worldclim database, annual

precipitation of Adaba-Dodola forest had also increased with elevation, from 917.23 mm at 2678 m to 1059 mm at 2942 m and from 1059 mm at 2942 m to 1089.23 mm at 3232 m.

Table 1. Temperature and rainfall data at three sites in Adaba Dodola forest

Months	Keta forest site: 2565-2800 m (Lower elevation)				Deneba forest site: 2804-3115m (Middle elevation)				Bubisa forest site: 3120-3400 m (Upper elevation)			
	Average T-Max (°C)	Average T-Min (°C)	Average T (°C)	Average RF (mm)	Average T-Max (°C)	Average T-Min (°C)	Average T(°C)	Average RF(mm)	Average T-Max (°C)	Average T-Min (°C)	AT (°C)	Average Rf (mm)
Jan	21.04	8.16	4.60	25.63	18.49	5.94	12.21	27.40	17.85	5.61	11.74	24.77
Feb	20.64	7.77	14.21	37.00	17.92	5.36	11.64	39.83	17.08	4.83	10.97	38.73
Mar	21.27	8.40	14.84	66.60	18.46	5.90	12.19	78.60	17.41	5.17	11.29	78.87
Apr	20.88	8.02	14.45	111.33	18.32	5.76	12.04	128.83	17.20	4.97	11.07	148.67
May	21.69	8.41	14.86	88.43	18.40	5.84	12.14	109.87	17.34	5.10	11.22	124.30
Jun	20.66	7.79	14.24	71.90	17.30	4.74	11.02	84.27	16.30	4.05	10.17	78.53
Jul	21.48	4.75	13.11	131.80	17.88	3.31	10.60	145.63	17.11	2.39	9.75	129.17
Aug	20.66	4.93	13.30	135.87	17.52	2.96	10.24	146.77	16.75	1.70	0.39	145.10
Sept	21.42	4.71	13.07	114.23	18.24	3.69	10.98	135.40	17.48	2.74	0.10	138.80
Oct	21.30	4.59	12.95	84.23	18.96	4.42	11.69	101.30	18.15	3.41	0.78	117.60
Nov	20.83	4.11	12.46	31.37	18.45	3.91	11.18	38.73	17.68	2.94	0.31	45.53
Dec	21.55	4.84	13.18	18.83	18.50	3.96	11.22	22.37	17.88	3.14	10.51	19.17

T-Max= Maximum temperature; T-min= Minimum temperature; T= Temperature; RF= Rainfall
Source of data: Fick and Hijmans (2017): http://www. worldclim.org/version2

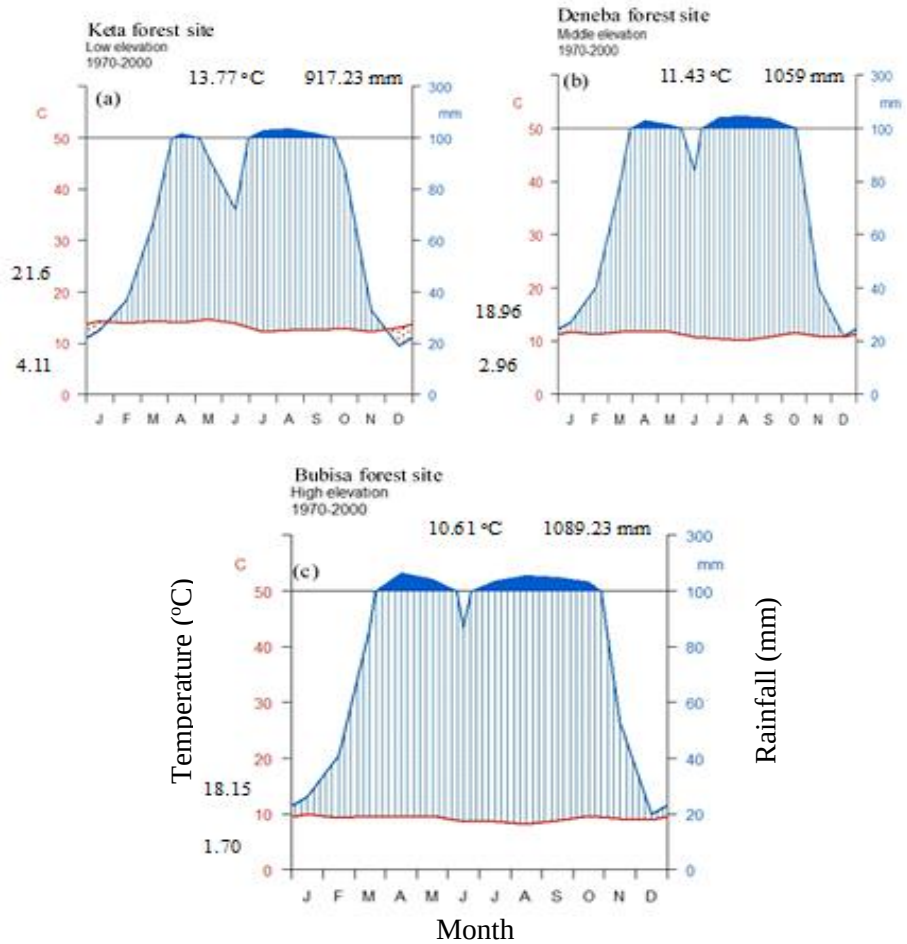


Figure 2. Climate diagram for three forest sites in Adaba-Dodola Afromontane forest for the period of 1970-2000: (a) Keta site (low elevation) (b) Deneba site (Middle elevation) (c) Bubisa site (upper elevation)

Source of climate data: Fick and Hijmans (2017): http://www. worldclim.org/version2

3.1.3. Topography and soils

There are two distinct topographic landscapes in the study area: the northern part, which is lacking of trees due to intensive cultivation, and the southern part, which is rough mountain landscape, covered by degraded forests (Asrat *et al*., 1997). The existing forests patches are located in inaccessible areas and marginal lands. The study area is the major water source of the Bale zone, which flows northwards to the River

Wabe Shebele and to the Genale-Dawa drainage basin to the south. The soils of the study site were of volcanic origin (Girma, 2006). They generally constitute well-structured silt or clay of more than 1 m depth on gentle slopes and valleys but are shallow on steep slopes and the tops of ridges (Asrat *et al.*, 1997). Mean soil pH of the study site was 5.9, mean soil moisture content was 0.49%, mean bulk density was 0.61 g/cm^3, mean OM was 7.48 %, mean electrical conductivity (EC) was 0.22 $mmhocm^{-1}$, mean total N was 0.49 %, and available phosphorus was 6.63 ppm ($mg\ kg^{-1}$). The soil pH (5.9) of the study area was considerably moderately acidic in general. Low soil pH on this site is supposed to be caused due to high precipitation prevailing in the study area that might be brought about leaching of basic nutrients, especially in the higher elevation zones. Based on the soil nutrient ratings made in the country by Tekalign (1991), the present soil analysis of the study site is characterized as high TN (%) and OM (%), moderately acidic pH and low available phosphorus.

3.1.4. Vegetation

Adaba-Dodola forest was classified as undifferentiated Afromontane forests by Friis (1992); as upland evergreen mixed forests by Friis and Tadesse (1990); as upland dry evergreen forests by Friis *et al.* (1982) and as coniferous and mixed forests by Russ (1979). The forest formation changes along the altitudinal gradient revealing the strong dominance of conifer forests 2565 to 2800 m, where *Podocarpus* and *Juniperus* ruled over all other species (Figure 8). At the middle altitude of between 2804-3115 m, *Juniperus procera* is dominant in association with other broadleaf hardwood species. *Podocarpus falcatus* occurs less in this altitude and sporadically found at the lower margin of this zone. At the upper elevation zone, 3120-3400 m, *Hagenia abyssinica*, *Hypericum lanceolatum* and *Erica arborea* dominated the forest formation. Other

indigenous tree species found in the forests include *Olea europea, Allophylus abyssinicus, Nuxia congesta, Ekebergia capensis, Scheffleria abyssinica, Buddleja polystachia, Maytenus* species, etc. There are also enrichment plantings of exotic species of *Eucalyptus* species and *Cupressus lusitanica* in the peripheral areas, on former logging sites and around homestead.

Five species were frequently and dominantly distributed at different elevation zones of Adaba-Dodola Afromontane forests. These species include *Podocarpus falcatus, Juniperus procera, Hagenia abyssinica, Erica arborea* and *Hypercum revolutum*. The former two species were predominantly distributed in the low and middle elevations while the latter two species were predominantly distributed in the middle and high elevation zones. They were the key indicator species in Adaba-Dodola Afromontane forest communities at distinct elevation gradients. The ecological characteristics of the five major species are described below:

Juniperus procera is an Afromontane tree reaching up to 45 m at maximum height in the study site. Up to 50 m height is also reported in some other Afromontane forests, it is the largest tree of its genus. It flowers and sets seeds only periodically and the flowers are inconspicuous. It is a dioecious and wind pollinated tree with grey or glaucous leaves when matured. The distribution zone of *Juniperus procera* largely coincides with that of *Podocarpus falcatus*. *J. procera* is susceptible to fire because it is flammable. The biophysical limit of the species in the study area was up to 3100 m altitudinal range, up to 1069 mean annual precipitation range and up to 11 ^{o}C mean temperature ranges in the present study. The species was also distributed on well-drained soils and on nearly neutral pH soils.

Figure 3. *Juniperus procera* (date of photo: Feburary 8, 2016)

Podocarpus falcatus was the dominant species in Afromontane areas, especially at low elevation of the study area. Ecologically, the vegetation within which *Podocarpus falcatus* is found includes transitional rainforest, dry evergreen forest and Afromontane rainforest. *P. falcatus* is particularly a characteristic of undifferentiated Afromontane forest, where it is one of the dominant species in *Podocarpus* forest or one of the co-dominant species in *Juniperus-Podocarpus* forest, often persisting in remnant forest patches in gully forests and church forests. This tree is frequent as a single tree left in derived grassland or in farmland in areas with sufficient rainfall. A humid and warm climate is preferable but in dry and hot areas, plantations fail (Orwa *et al*., 2009). The biophysical limits of the tree distribution in the Adaba-Dodola forest was up to an altitude range of 3100 m, mean annual temperature of up to 11^{o}C, mean annual rainfall of up to 1059 mm and on the well-drained soils.

Figure 4. *Podocarpus falcatus* (date of photo: Feburary 15, 2016)

Hagenia abyssinica is also an Afromontane forest, which was distributed from middle to upper elevation zones. Based on its botanical description, *Hagenia abyssinica* is a tree up to 26 m tall, with thick branches, branchlets covered with silky brown hairs and ringed with leaf scars. Biologically, Hagenia trees have either male or female flowers. Flowering and seeding can be observed throughout the year with a break in the months during the coldest temperatures.

Ecologically *Hagenia abyssinica* was first described in Ethiopia and distributed in East Africa (Bekele-Tessema, 2007). The same author mentioned that it occurs in undifferentiated Afromontane forest (Juniperus-Podocarpus forest) and dry single dominant Afromontane forest (Juniperus forest or forest dominated by Hagenia) in the upper limit. It was found often associated with *Schefflera volkensii, Galiniera saxifraga, Myrsine melanophloeos, Hypercom revolutum* and *Erica arborea* trees in Adaba-Dodola forest.

Figure 5. *Hagenia abyssinica* (date of photo: Feburary 8, 2016)

Hypercum revolutum is an Afromontane tree mainly distributed in the middle to high elevation zones. *Hypercum revolutum* is a tall tree (can reach up to 16 m in study area) of Afromontane forest often associated with *Erica arborea* and *Hagenia abyssinica* in the upper elevation zones of 2200–3700 m (Bekele-Tessema, 2007). However, in Adaba-Dodola Afromontane forest its distribution ranged from 2800-3400m. According to Bekele-Tessema (2007), Hypericums are readily propagated from seed, cuttings, rooted runners for species that help them quickly spread. In the study area, it has been mainly used as firewood and timber production.

Figure 6. *Hypercum revolutum* (date of photo: Feburary 11, 2016)

Erica arborea is another Afromontane forest of a typical African highlands forest. It grows on dry rocky ground with thin soils in moist and upper elevation zones up to 2500–3300 m (Bekele-Tessema, 2007). In the current study areas, its altitudinal distribution range was from 2800-3400 m. It is a shrub or tree with much-branched evergreen with height of up to 5 m based on past studies (Bekele-Tessema, 2007). However, in the present study up to 24-meter height was recorded, especially in the upper end zone of the elevation. *Erica arborea* has abundant and white-pink flower.

Figure 7. *Erica arborea* (date of photo: Feburary 11, 2016)

Adaba-Dodola vegetation is varied based on elevational variability as depicted in Figure 8. Topographic, edaphic and anthropogenic factors (Slope degree, elevation soil moisture, total nitrogen, grazing and cutting) were the significant driving factors for the variation as identified by the canonical ordination and multivariate models in the present study. Elevation was observed more important than the rest of the environmental variables in affecting pattern of woody plant distribution. Because there are large environmental changes across a relatively short elevational range (Körner, 2007). For example, elevation drives drastic changes in abiotic factors such as water, temperature and soil properties (Körner, 2000). Consequently, environmental and climatic factors migt palayn a role in filtering the coexisting species that have similar physiological tolerances.

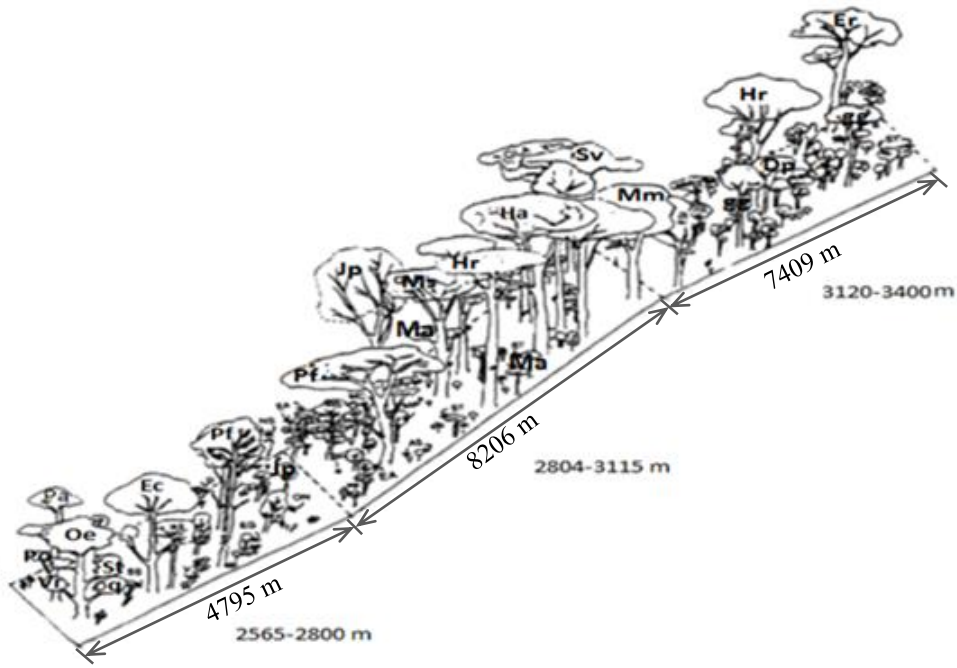


Figure 8. Profile diagram of the Adaba-Dodola Afromontane forest in three study sites

Profile diagram of the Adaba-Dodola Afromontane forest at three forest sites (Keta forest site: 2565-2800 m; Deneba forest site: 2804-3115 m; Bubisa forest site: 3120-3400 m). Ha= *Hagenia abyssinica;* Jp= *Juniperus procera;* Hr= *Hypercum revolutum;* Ms=*Myrica salicifolia;* Or= *Olinia rochetiana;* Pf=*Podocarpus falcatus;* Ec=*Ekebergia capensis;* Pa=*Prunus africana;* Sv= *Schefflera volkensii;* Er=*Erica arborea;* Dp=*Discopodium pennlnervium;* Mm= *Myrsine melanophloeos;* Gg= *Gnidia glauca;* Ma= *Maytenus undata;* Ml= *Maesa lanceolate;* Oq= *Osyris quadripartite;* Ra= *Rosa abyssinica;* Vr= *Vernonia rueppellii;* St= *Scolopia theifolia;* Oe= *Olea europaea*

3.1.5. Anthropogenic activities

Adaba-Dodola forest is undergoing rapid changes and is facing large-scale anthropogenic disturbances in the form of grazing or browsing, agricultural expansion, frequent tree felling (cutting), widespread lopping and human settlement encroachment. Most forests have been cleared and replaced by cultivation of cereal crops. The anthropogenic disturbances have progressively reduced the size of the forest from 140,000 ha in the early 1980s to 53,000 ha in 1997 (Kubsa *et al*., 2003). According to Tadesse (1999), the rate of annual deforestation in Adaba-Dodola forest was 3% between 1993 and 1997.

Today, it is common to see barley cultivation at altitude of 3400 m and above, which was beyond the limit of barley production (Friis, 1992). This shows that the temperature is rising in the area and thus made the area suitable for expansion of cereal cultivation. Such progressive encroachment of cultivation is primarily due to increasing human demographic pressure. Adaba-Dodola forest is a very fragmented forest mainly due to scattered settlements within the forests (eg. Figure 9a) consisting of about 4,000 households. Adaba-Dodola district has the population of about 200,000 persons with 40,000 households as reported by IFMP (2000a). There are about 4000 households (or 20,000 people) inhabiting the remaining forest patches (IFMP, 2000a).

The livelihood of forest dweller communities in Adaba-Dodola depend on forest and forest products. The community produce four major types of wood products for home level consumption and for market sale. These include fuel wood, smoothened Juniper poles which is locally called *Kanchi* (Figure 9c), rough Juniper poles, *Xarbi* and lumber. Juniper poles are products used locally for the construction of houses and fences. Pit sawing is the traditional method of wood processing widely used by forest dwellers, especially in low and mid elevations. Damesa (2002) reported that the recovery rate of trees employing this method was to be 30 %. The most preferred trees for pit sawing and other wood processing are *Juniperus procera, Podocarpus falcatus* and *Hagenia abyssinica. Juniperus procera* is particularly highly valued by the forest users for all kinds of usage such as construction, furniture and firewood.

For all households of the forest dwellers, wood is the major source of energy for cooking and heating. The firewood is collected from the close forests to the settlement areas. The annual consumption of firewood per person in the study area is 0.5 m^3 (WBISP, 2001). In addition to the household consumption, firewood is also the main source of additional income. Shiferaw (2003) reported that 50 % of the forest

dweller households in Adaba-Dodola forest sell two donkey loads of firewood every week. The same report indicates that the remaining 50 % of the households located at higher altitudes do not sell firewood because the local markets are too far away.

For communities residing in the forest, grazing in the forest is the only means for the user groups to maintain their livestock. During the rainy season, the livestock are kept at the lower altitudes on open grazing grounds. Forest grazing is particularly important during the dry season when the availability of fodder on the open pasture is exhausted (Girma, 2006).

The major kinds and species of livestock kept by the forest dwellers are cattle, sheep, horses, donkeys and goats. A total of 97 % of the forest user group members possess some kind of livestock (Schmitt, 2003). The average holding is 14 head of livestock per household (Girma, 2006). The impact of grazing on the forest vegetation varies with the livestock type and the tree species. Goats cause the greatest amount of damage to young browsable plants. Previous studies conducted in the area reported that the two indigenous conifer species, *Juniperus procera* and *Podocarpus falcatus*, are less sensitive to browsing (Tesfaye *et al.,* 2002; Regassa, 2003). The studies also indicated that grazing reduced mainly the young regrowth of broadleaf species. *Hagenia abyssinica*, in particular, is very palatable by all types of livestock implying that it is advisable to regulate grazing in the broadleaf dominated parts of the forests.

Figure 9. Anthropogenic activities in Adaba-Dodola Afromontane forest: (a) settlement and cultivation (b) grazing (c) tree cutting for fencing crop field and *Kench* (smoothened Juniper splits*)*

3.2. Site selection

This study focused on the Afromontane forest in the Adaba-Dodola district, Southeastern Ethiopia. Before the actual inventory, a reconnaissance survey was carried out to obtain the general overview of the vegetation and to identify the appropriate sampling sites for the study. Based on classification by Friis (1992) and field reconnaissance survey, the study area was divided into three homogenous zones in relation to elevation and vegetation features: lower elevation areas with *Podocarpus* forest dominance (Keta forest site); mid elevation areas with dominance of *Juniperus* forest mixed with broadleaf species and relatively less disturbed forest (Deneba forest site); upper elevations with mainly dominated by *Erica-Hypericum* forest (Bubisa forest site). In all forest sites, agricultural activities and settlement were intensively practiced.

3.3. Data collection

3.3.1. Environmental and meteorological data collection

Environmental variables such as elevation, geographical coordinates, slope, aspect, slope position and soil data for chemical and physical properties (pH, total nitrogen, OM, Available P, EC, bulk density, soil moisture) were collected from each plot (Table 2). Elevation and geographical coordinates were measured using Garmin eTrex GPS-65. Slope and slope aspect were measured using a compass meter.

Soil was sampled using auger for bulk density analysis, and knife, measuring tape and spoon for chemical and seed bank analysis. For bulk density assessment, three soil samples were taken diagonally from each main plot. An auger of 8 cm in diameter was used to take soil sample from a surface soil of 7 cm depth. A total of 270 soil

samples were taken and composited into 90 samples (a composite of three diagonal samples from each plot) for bulk density analysis (Figure 10).

For soil chemical analysis, three samples were collected from each plot from the depths of 20 cm (Figure 10). During collection of samples, dead plants and compost pits were excluded and one composite soil sample was then prepared for each plot. Hence, a total of 90 composite samples were considered to minimize differences among samples. The three samples from each plot were mixed and samples were prepared for analysis.

Meteorological data, temperature and precipitation, were extracted from free global climate data-WorldClim for the period of 1970-2000 (http://worldclim.Org /version2). The patterns of precipitation and temperature in three sites (Keta forest, Deneba forest and Bubisa forest) were indicated in Table 1 and Figure 2. The climate diagram was computed using R for windows statistical package.

Table 2. Environmental explanatory variables used in the study

Dependent variables	Explanatory variables
Species composition	Environmental variables
Species diversity	Topographic factors
Species richness	Elevation
Basal area	Slope
Density	Aspect
	Edaphic factors
	pH
	Available Phosphorus
	Total Nitrogen
	Organic matter
	EC
	Soil moisture
	Soil bulk density

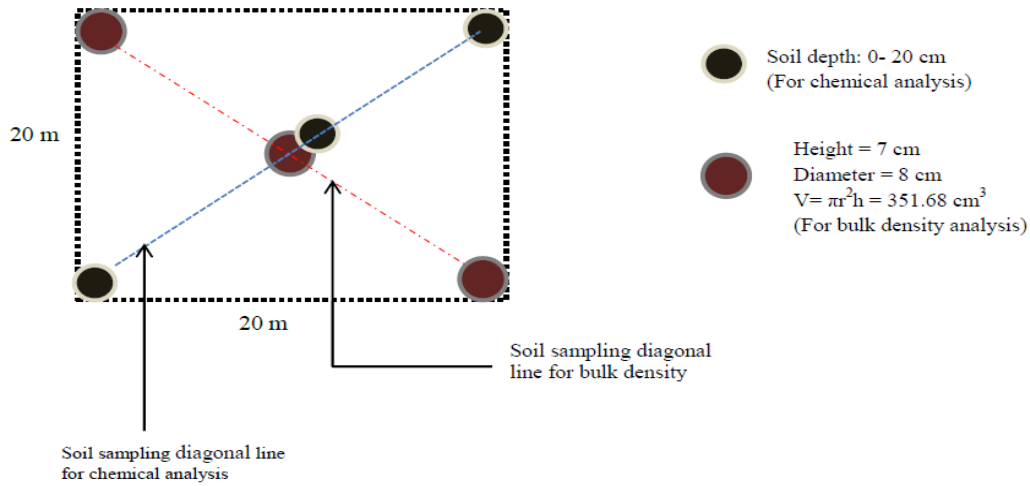


Figure 10. Soil sampling plot lay out for bulk density and chemical analysis

3.3.2. Vegetation data collection

Considering time, logistics, research objectives and accessibility of the fragmented vegetation, we decided to sample 30 plots from each of the three forest sites on two transects (with minimum of 1 km apart) that pass through the longest side of the forest to accommodate the lower and upper end of the forest (Figure 12a-c). The size of the three forest sites were 1,064 ha, 2,017 ha and 4,219 ha for Keta, Deneba and Bubisa, respectively. Vegetation was sampled from a total of 90 plots along elevation gradient from the bottom of 2565 m to top 3400 m.

To explore the compositional and diversity patterns of Afromontane forests and evaluate the relative impact of anthropogenic and environmental factors, the three sites were assessed along elevation gradient from bottom to up. Plots of 20 m x 20 m (400 m^2) were established to record the number of individuals, diameter at breast height (DBH), heights, canopy cover and canopy openness of all individual plants with DBH ≥ 2 cm. Nested plots measuring 5 m x 5 m and 2 m x 2 m were established

randomly within a main plot at a corner to sample all individual saplings (DBH < 2 cm and height of 1- 2 m) and seedlings (DBH < 2 cm and height ≤ 1 m) (Figure 11a).

All woody plant species encountered in each plot were recorded and named by their vernacular names in the field with the help of a local expert. Scientific names were also given in the field whenever possible with the assistance of Botanist using plant identification manuals. For those species difficult to identify in the field, specimens were collected, pressed and transported to the Ethiopia Biodiversity Institute (EBI) for taxonomic identification. Previous published volumes of the Flora of Ethiopia and Eritrea were used to identify the specimens (Hedberg and Edwards, 1989; Edwards *et al*., 1995; Hedberg and Edwards 1995; Edwards *et al*., 1997; 2000; Hedberg *et al*., 2004)

Canopy cover was estimated for each woody plant and expressed as the percentage of a plot area covered by the canopy of woody plants. Canopy openness was measured for each woody plant (DBH ≥ 2 cm) encountered in the plot directly in the field by spherical densiometer and expressed as the percentage of open canopy. The spherical densiometer had 24 grids (squares) with 4 dots in each square amounting a total of 96 dots **(**Figure 11b). Readings were taken for each woody plant in a plot in two directions and the number of dots not covered by canopy in the grids was counted and converted into percentage by multiplying the number of uncovered dots by 1.04 (i.e., number of dots covered by closed canopy × $\frac{100}{96}$). The mean percentage of canopy cover readings from the two directions were taken for analysis.

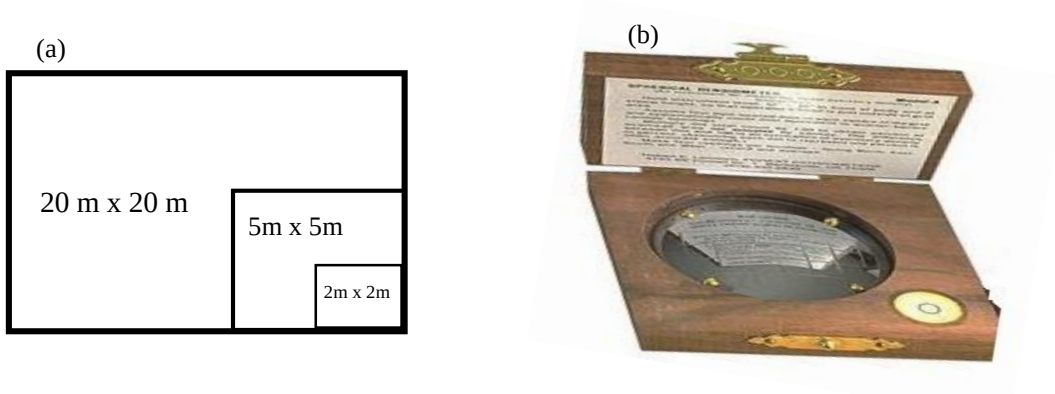


Figure 11. (a) Layout of a nested plot used in vegetation data sampling (b) Spherical densiometer used to measure canopy openness

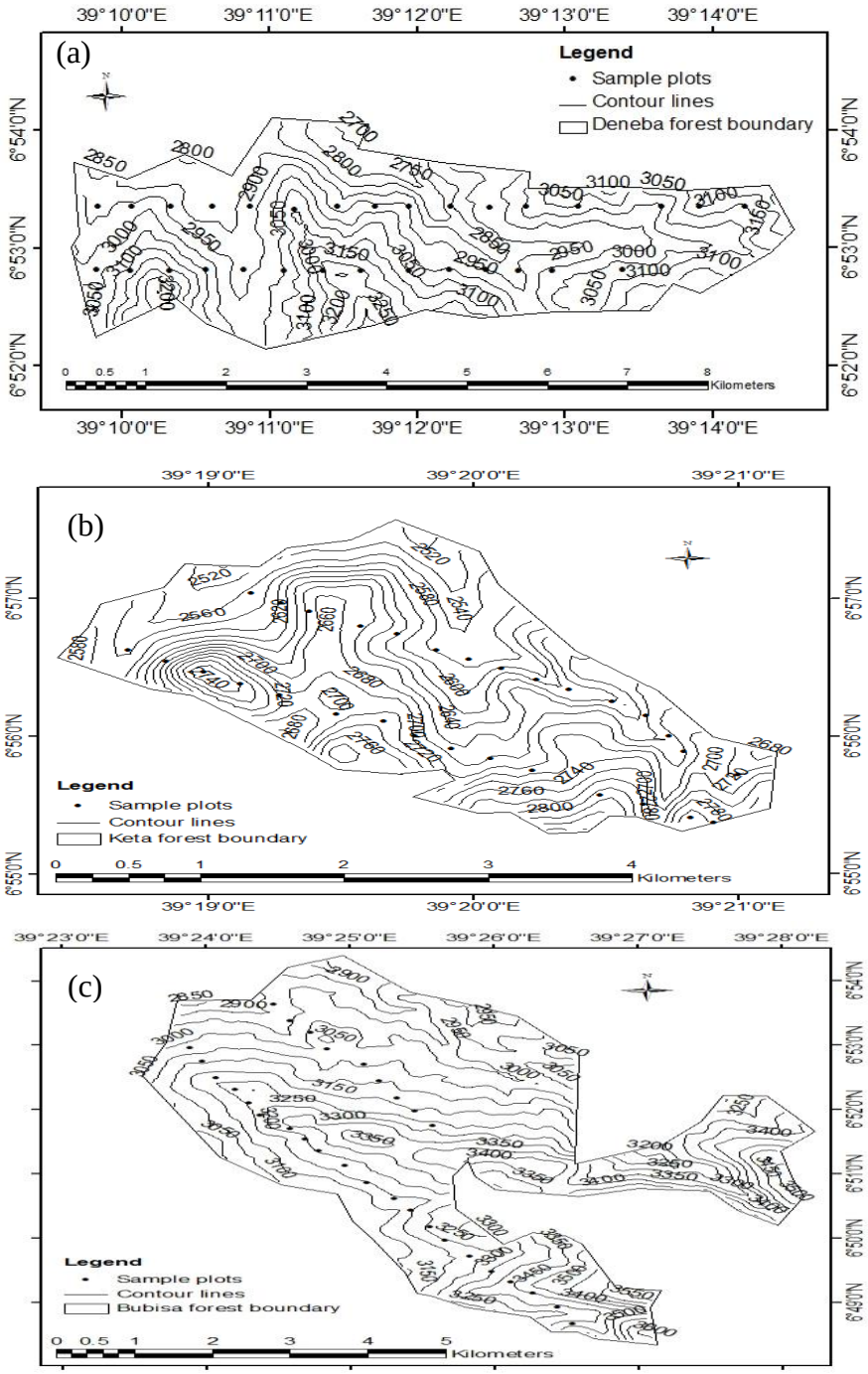


Figure 12. Study forest site boundaries, contour lines and sampling plot deployment on transect lines in (a) Deneba forest site (b) Keta forest site (c) Bubisa forest site

3.3.3. Soil seed bank data collection

To investigate the soil seed bank (SSB), three sub-plots with area of 100 cm^2 were sampled at two end corners and at the center of the diagonal line of the main plot used for vegetation sampling (Figure 13). Soil samples were collected diagonally from three separate soil layers (0-3 cm, 3-6 cm and 6-9 cm) using a knife, a spoon and a meter. The rationale for taking the soil samples at the three soil layers was to examine variations in soil depth (Demel and Mulugeta, 2006). The depth of each layer was taken following the methodology used by Feyera and Demel (2002) and Getachew *et al*. (2004). Soil samples from the same layers of the three sub-plots of the same plot were mixed, pooled and put in one plastic bag and formed a composite sample. The composite samples were used as the working sample for germination study. Accordingly, total of 270 pooled samples were (90 plots x 3 layers) used for seed bank germination test in Arsi University greenhouse, Ethiopia (Figure 14). Sampling was performed in the months of February and March 2016 at the onset of seed production season but before the onset of germination season.

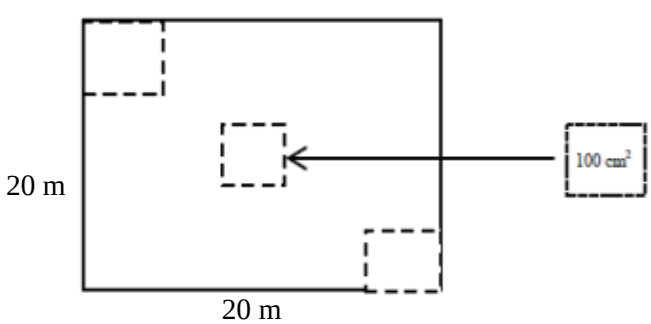


Figure 13. Nested plots within the main plot for soil seedbank sampling

Figure 14. Soil seedbank experiment in the greenhouse

3.3.5. Anthropogenic disturbance data collection

All possible anthropogenic disturbance types were identified based on discussions with local forest users and field observations. The major anthropogenic disturbance types that were occurring frequently and having multiple effects on Adaba-Dodola Afromontane forest were identified as cutting / lopping, grazing / browsing, human settlement, agricultural expansion and roads. All the disturbance factors were recorded for each plot and estimated based on approaches of Sagar *et al.* (2003), Zhu *et al.* (2007) and Popradit *et al*. (2015). The disturbances related to settlement, agriculture and road were evaluated based on the distance of the sampled plot from the nearest village, agricultural field and main road, respectively. Effect of cutting disturbance was estimated by the relative density of tree and shrub cuts (stumps)

in each plot. The individual tree and shrub cuttings (stumps) were counted in each plot (20 × 20 m) against total tree individuals in the plot to calculate the relative density. The relative density was estimated as:

Relative density of cuttings (stumps) = total number of stumps (cut individuals) in a plot / total number of individuals in a plot × 100.

Grazing (browsing) impact was estimated based on relative density of grazed (browsed) seedlings and saplings in each plot.

Relative density of grazed seedling and sapling = total number of seedling and sapling grazed (browsed) in a plot / total number of seedlings and saplings in a plot × 100.

Agricultural and road disturbance variables were excluded from multivariate analysis model to avoid duplicate information because the collinearity analysis test indicated that both agricultural and road factors had strong collinearity with settlement and each other.

Table 3 Anthropogenic disturbance explanatory variables used in the study

Response variables	Explanatory variables
Species composition	Anthropogenic disturbance variables
Species diversity	Cutting
Species richness	Grazing/ browsing
Basal area	Agriculture
Density	Settlement
	Road
	Canopy openness

3.4. Data analysis

3.4.1. Analysis of species richness and diversity

Species richness is used as the number of species per plot (Curtis and McIntosh, 1951).

The diversity indices were calculated following (Kent and Coker (1992):

Shannon Wiener diversity index: $H' = -\sum_{i=0}^{s} pilnpi$ (1)

Where *pi* is the proportion of individuals found in the i^{th} species.

Evenness (E) index: $E = H'/H_{max} = H'/\ln S$ (2)

Where H_{max} denotes the maximum level of diversity and *S* is number of species.

Beta diversity (Whittaker, 1972): $\beta_w = \frac{Sc}{S} - 1$ (3)

where β*w* is Whittaker beta diversity, *Sc* is the number of species in the composite sample (number of species in the whole data set), and *S* is the mean species richness (α-diversity) in the sample units. If β_w is 0 then all considered plots (communities) similar species. β*w* < 1 is considered as low and βw > 5 is considered high (McCune and Grace, 2002). The largest value for β*w* is observed when no similar or the same species among communities or plots.

Species turnover (β_T) between gradients was determined as the gain and loss of species according to the formula proposed by Wilson and Shmida (1984):

Beta diversity (species turnover): $\beta_T = \frac{g(H) + l(H)}{2\alpha}$ (4)

Where *g* (*H*) and *l* (*H*) are the number of species gained and lost along the gradients, respectively and α is the mean species richness of adjacent site / elevation gradients. A high β value indicates high species turnover and less similarity between the compared units (Porembski *et al*., 1996). A low β value indicates high habitat similarity between the compared study units. Species richness over a range of habitats (landscape, geographical area) is called gamma (γ) diversity (Moreno and Halffter, 2001; McCune and Grace, 2002).

Sorensen's Similarity Index: $S = \frac{2C}{(A + B)}$ (5)

C = shared species by *A* and B sites, *A* = the number of species in one site; *B*= number of species in other site (Bray and Curtis, 1957).

3.4.2. Forest stand structure analysis

A forest stand structure is characterized by forest diameter distribution, stand height, stand density, basal area, stand volume and other quantitative of information collected from forest inventories (Brodbeck, 2004). For characterizing the forest structure and natural regeneration for this study, the diameter distribution, the basal area, floristic composition, plant density, plant frequency, importance value index and plant vertical and horizontal structures were analyzed. All individuals of trees and shrubs with a diameter at breast height (DBH) ≥ 2 cm and height greater than 2 m were measured for DBH. All individuals of seedlings and saplings were counted in each plot.

Horizontal structural analysis of trees was determined by grouping individual trees by 10 cm diameter classes intervals (≤ 10, 10.1-20, 20.1-30, 30.1-40, and 40.1-50, etc.) to graphically portray the diameter distribution. The vertical stratification analysis of trees was examined using the International Union of Forest Research Organizations (IUFRO) classification method (Lembandgut, 1958; cited in Lamprecht, 1989). According to this method, the top height was used for determining the vertical structure. Tree with >2/3 height of the top represents upper storey, tree with height between 1/3 and 2/3 of the top height represents the middle storey, and the lower storey is represented by trees with height < 1/3 of the top height.

Density (i.e., the number of plants of a certain species per unit area) was expressed by changing individual number per plot into the hectare basis. Basal area (BA) calculation was made on the diameter measurements of the tree stems with DBH of ≤ 2 cm and expressed in square meter per hectare (m^2 / ha). Frequency was expressed as the number of quadrats occupied by a given species per number thrown (Goldsmith *et al*., 1986). The forests structure was depicted using histogram and charts for both

diameter and height class distributions which was then interpreted as an indication of regeneration status.

The Importance Value Index (IVI) permits a comparison of species in a given forest and depicts the sociological structure of a population in its totality in the community. It often reflects the extent of the dominance, occurrence and abundance of a given species in relation to other associated species in an area (Kent and Coker, 1992).

The forest structural analysis indexes were calculated based on the following formulae.

$$B_A\,(m^2) = (D_{BH} \div 200)^2 \times 3.14 \quad (6)$$

$$R_F = (F_s / T_S) \times 100 \quad (7)$$

$$R_D = (N_i / T_n) \times 100 \quad (8)$$

$$R_{Do} = (D_s / T_D) \times 100 \quad (9)$$

$$I_{VI} = R_D + R_F + R_{Do} \quad (10)$$

Where, I_{VI} is the importance value index; R_D is relative density; R_{Do} is relative dominance; R_F is relative frequency. N_i is number of individuals of a species in the sample; T_n is total number of individuals of all species in the sample. F_s is frequency of a species in the sample; T_s is total frequency of all species in the sample. D_s is dominance of a species; T_D is total dominance of all species in the sample; B_A is basal area; D_{BH} is the diameter (cm) at breast height.

3.4.3. Soil physico-chemical analysis

For soil bulk density analysis, 90 composite soil samples were oven dried with a temperature of 105 ^oC for 24 hours. The soil bulk density (BD) was calculated as the ratio of oven dried soil weight to the volume of the soil:

$$BD = \frac{Wd}{V} \quad (11)$$

where *Wd* is weight of oven dry soil (g) and *V* is volume of the soil (cm^3). The volume of the soil was calculated from volume of the auger.

For soil chemical analysis, a total of 90 composite soil samples were air-dried, mixed well and passed through a 2 mm sieve for selected soil chemical analysis. The pH of the soils was measured in water suspension in a 1:2.5 (soil: liquid ratio) potentiometrically using a glass-calomel combination electrode (Van Reeuwijk, 1992). Total N was analyzed using the Kjeldahl digestion, distillation and titration method as described by Black (1965) by oxidizing the OM in concentrated sulfuric acid solution (0.1N H2SO4). The electrical conductivity (EC) of soils was measured from a soil water ratio of 1:2.5 socked for one hour by electrical conductivity method as described by Sahlemdhin and Taye (2000). The Walkley and Black (1934) wet digestion method was used to determine soil carbon content and the percent soil OM was obtained by multiplying percent soil OC by a factor of 1.724 following the assumptions that OM is composed of 58% carbon. Since the Olsen method is the most widely used for P extraction under wide range of pH both in Ethiopia and elsewhere in the world (Landon, 1991; Tekalign and Haque, 1991), available soil P was analyzed according to the standard procedure of Olsen *et al.* (1954) extraction method.

3.4.4. Soil seed bank analysis

A total of 270 samples were taken to the greenhouse on the premises of Arsi University, Ethiopia, where they were incubated to stimulate germination of seeds. The soil samples were spread in plastic trays and placed randomly on shelves in a greenhouse and kept continuously moist with tap water. Emergent seedlings that were readily identifiable were identified, counted and discarded. Those seedlings that were difficult to identify at emergency period were marked and kept until identification was possible. After six months course of germination test in the greenhouse, the experimentation was ceased as no new germinated seedlings were observed for two

consecutive weeks. Those seedlings that were still difficult to identify in the greenhouse were transported to the Herbarium of Ethiopian Biodiversity Institute for identification.

Seed bank species density was calculated from seedling counts, expressed in m^2 for each soil depth (layer). Species composition (number of species germinated) and density (number of germinated seedling per square meter) of the soil seed banks among the study communities and between soil depths were computed by GLM model using SPSS 22 (SPSS Inc., USA). Seed bank attributes were introduced as dependent variables, while depth (0–3 cm, 3– 6 cm and 6–10 cm) and cluster categories were introduced as fixed factors. The similarity between species composition in the seed bank and aboveground vegetation was calculated using Jaccard's similarity index (Greig-Smith, 1983). This coefficient was calculated for aboveground and soil seed bank woody vegetation by the formula:

$$S_{j\,(A,\,B)} = \frac{a}{a+b+c} \qquad (12)$$

where *a* is the number of common species in sample A and sample B, *b* is the numbers of species present in A, but absent in B, *c* is the number of species present in B, but absent in *A*.

3.4.5. Cluster and ordination analysis

Clustering was used to categorize vegetation attributes together (sample units and species) based floristic similarities (Kent and Coker, 1992; McCune and Grace, 2002). Species abundance data was used for clustering. Initially, abundance value was calculated at an elevation interval of 10 m and then the species were clustered using Ward's group linkage method, and relative Euclidean distance as the similarity

measure using PC-ORD software (McCune and Mefford, 1999). To minimize the the variations within the group tahna among the group, the Ward's method was used. The Euclidean Distance was used as it avoids the differences among sample units (Tabachnick and Fidell, 2001).

To detect and describe the indicator species for environmental conditions, indicator species was calculated following Dufrêne and Legendre (1997). Accordingly, species indicator values were used to identify the indicator species of the group and their statistical significance for groups. The indicator species calculation consists both the information of species abundance and frequency of occurrence of a species in a particular group (McCune and Mefford, 1999). Indicator values were tested for statistical significance using a Monte Carlo test technique. The indicator values range from zero (no indication) to 100 (perfect indication). Based on the indicator species analysis (ISA) and the Multi-Response Permutation procedure (MRPP) methods, four clustered groups of similar in floristic composition were identified along elevation gradients.

Differences in the floristic compositions among the identified plant communities or groups were analyzed with nonparametric multi-response permutation procedures (MRPP). MRPP is a nonparametric multivariate test that avoids the normality requirements of parametric multivariate tests (McCune and Grace, 2002). In MRPP, the Euclidean distance among the plant communities was used. The ***P*** value and test statistic ***T*** were evaluated if the variations among groups were significant or not. The chance-corrected within-group agreement (A) used to see within group homogeneity. The test statistic, ***T*** describes the separation between groups (communities or clusters) with more negative values indicating stronger separation. The test statistic ***T*** was calculated as: $\boldsymbol{T} = (\delta_{observed} - \delta_{expected})/ \delta_{expected}$. Within-group

homogeneity was determined by within-group agreement, $\boldsymbol{A}$ and calculated as $\boldsymbol{A} = 1 - (\delta_{observed}/\delta_{expected})$. $\boldsymbol{A}_{maximum} = 1$ when all items are identical within groups (delta = 0; i.e., $\Delta\delta_{observed} = 0$) and $\boldsymbol{A} = 0$ when heterogeneity within groups equals expectation by chance ($\delta_{observed} = \delta_{expected}$), and $A < 0$ when heterogeneity within groups is higher than the expected by chance ($\delta_{observed} > \delta_{expected}$) (McCune and Grace, 2000).

Ordination is a method that used to expresses the relationships of several species and environmental variables together using a low-dimensional space using ordination diagrams (ter Braak, 1995; McCune and Grace, 2002). In the present analysis, the Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA) and Redundancy Correspondence Analysis (RDA) were used. The abundance data of species were used for analysis with these ordination techniques using PC-ORD (version 6.0; MjM Software, Gleneden Beach, Oregon, USA). The choice of appropriate analysis tool depends on the response of species to gradients where linear response or unimodal response (best performance around some environmental optima). According to McCune and Grace (2000), a maximum gradient length greater than 4 standard deviation (SD) in the DCA axis indicate a strong unimodal response between the species and environmental gradients, whereas gradient length less than 3 SD indicates linear relationship, anduse of Redundancy Analysis (RDA) is recommended. Lepš and Šmilauer (1999) also stated that the length of the gradient from the first analysis serves as a lead for selecting between RDA and CCA. Gradients sufficiently longer than 2 SD would justify the use of CCA, which assumes species have a unimodal response to the environmental gradients at this gradient length (standard deviation, SD) (ter Braak 1995).

In the present study, the initial test of data with DCA for whole community in the complete elevation indicated that the DCA axis gradient was 4.68 SD and hence Canonical Correspondence Analysis (CCA) was used (Jongman *et al*., 1987; Peck,

2010) for whole community analysis. However, for the clustered community the test of clustered data with DCA showed that the DCA gradients were less than 4 SD, justifying the use of RDA. The CCA ordination was done by log transformation of the abundance data to account for the large differences in species abundances (Schmitt *et al*., 2010) for whole community ordination. Species-environment correlations of the CCA axes were tested by Monte Carlo permutation test of 999 runs. Canonical coefficient was calculated to explore the extent of variation in the vegetation response that was related to each of the explanatory variables.

3.4.6. Multivariate statistical model analysis

Before data analyses, most predictor variables were transformed by log10(x) for continuous data (pH, AvaP, OM, Settlement distance), arcsine for proportional data (CO), SQRT(x+0.5) for count data (stump density, seedling and sapling density) to improve their normality. The aspect measured in degrees was converted to scales from 0 to 1, following the formula (1-cos(Ø -45)/2, where Ø is aspect in degrees, east of true north, with 0 value indicating the coolest slope (north west) and 1 indicating the warmest slope (southeast) (Mamo *et al*., 2013). Before data analysis, highly collinear variables from each set of explanatory variables (environmental and disturbance variables) were excluded to reduce the redundant information. Collinearity was detected using pairwise Pearson correlation analyses (Quinn and Keough, 2002) in order to avoid duplication effects caused by multi-collinearity (Dormann *et al*., 2013). The variable pairs that had correlation coefficients greater than 0.7 were omitted from the multivariate analysis and the variable having lower correlation with the other variables was retained (Sály *et al.*, 2011). Moreover, multi-collinearity among the variables was considered by evaluating variance inflation factors (VIF) during

Canonical model analysis using CANOCO software for windows. Highly collinear variables were omitted from further analysis, mostly VIF >10 are usually considered as high collinear and avoided from analysis.

To investigate the patterns of species composition and distribution and variation in species richness and diversity, the environmental gradients (elevation, slopes, aspects, soil edaphic factors) and anthropogenic disturbance factors such as cutting, grazing, settlement and canopy openness were recognized as potential drivers of species composition, distribution, diversity and richness. In the process of explaining the variation in vegetation pattern along the elevational gradients, it is important to determine the relative influence of predictors. Establishing relationships between species patterns and environmental characteristics is a major goal in the investigation of the driving forces of species distributions.

Canonical ordinations such as redundancy analysis and canonical correspondence analysis are invaluable tools for modelling communities through environmental predictors. They provide the means for conducting direct explanatory analysis in which the association among species can be studied according to their common and unique relationships with the environmental variables and other sets of predictors of interest. Legendre and Anderson (1999) noted that canonical analyses such as redundancy analysis (RDA) and canonical correspondence analysis (CCA) are vital tools for modeling communities through environmental predictors. Pedro (2006) stated that studies applying over 1500 CCA / RDA in modeling species–environment relationships were published on reputable ecological studies and this can be best indicative as these methods of modeling species–environment relationships are successful. The same author described that RDA and CCA can be best understood as methods for extending multiple regressions involving multiple response variables and

a common matrix of predictors. Legendre (2007) also stated that the analysis of a descriptor such as community composition data is carried out by Canonical Analysis Model (RDA/CCA) as a function of different types of environmental and spatial variables.

Due to the expected complexity of evaluating the explaining power of the predictors in the whole community along complete elevation, we conducted analysis at two scales: (1) the whole forest community along the complete elevation gradient to evaluate overall pattern of species composition, richness and diversity in relation to predictors and (2) within separate four clustered communities to evaluate the explanatory power of the predictors in each separate community. The two groups of predictor variables (environment and disturbance) that were considered as a potential drivers of the vegetation composition, diversity and richness in the study area were tested in four distinct communities having distinct elevation gradients. This was to show that whether the potential drivers had similar power in influencing the species composition in different communities and elevation zones.

3.4.7. Variation partitioning

Variation partition was used to examine how disturbance factors and environmental parameters influence vegetation patterns separately and jointly. To select the appropriate multivariate tool, the DCA test was performed and the results showed that the gradient length (SD) of the ordination axis for data matrix of the entire community was 4.68. Therefore, a unimodal canonical model (CCA) in CANOCO software was selected to relate species composition with environmental variables in the entire community in complete elevation analysis. However, the DCA test of each of the four clustered communities showed that the gradient lengths were less than 4

SD implying to use a linear canonical model (RDA) in CANOCO. Variance partitioning for the species composition, richness and diversity pattern was performed by the multivariate constrained canonical linear model (RDA) (Rao, 1964) for clustered communities at separate elevations.

To identify the relative influence of the sets of explnanatory factors in the plants richness and diversity, a forward selection method was performed to select the best combination of explanatory variables (environmental and disturbance factors) that accounted for most variation in woody species richness and diversity (Glantz and Slinker, 1990). Variables can be retained or deleted based on their contribution to the model, i.e., the non-contributing variables were omitted from the model. By using this model, the total variation in the explanatory variable was partitioned into [a] pure effect of environmental variables, [c] pure effect of disturbances, [b] mixed variation due to the joint effects of environmental and disturbance variables and [d] unexplained (residual) variations.

Variation partitioning was then used to test and determine the likelihood of the sets of predictors in explaining patterns in plant composition, distribution, richness and diversity. Some disturbance and environmental variables may share a common structuring vegetation composition (Pedro *et al*., 2006). Thus, in the analysis, the amount of variation in the species data that was due to this common structuring had been extracted by both environmental and disturbance sets of explanatory variables. The more complete picture of the partitioning of the total variation of the species data is as follows (Figure 15). Compositional variation was partitioned on two sets of variables: the environmental and disturbance variables.

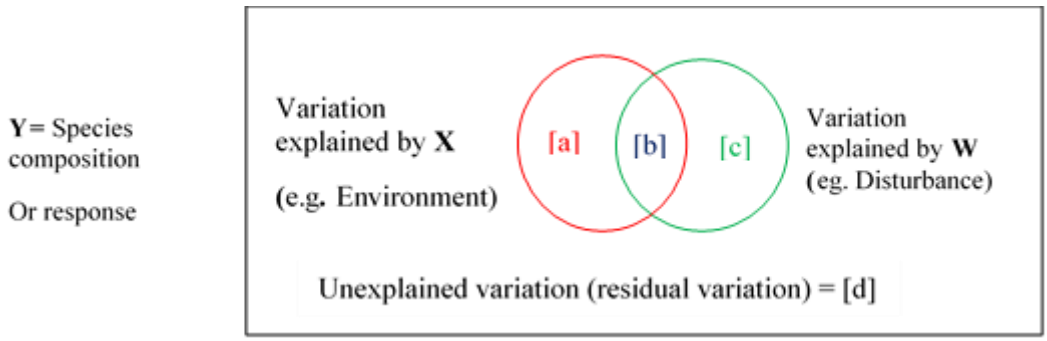


Figure 15. Venn diagram representing the partition of the variation of response and predictor

Venn diagram representing the partition of the variation of a response variables or a response matrix Y between two sets of Predictors X (e.g., environmental factors) and W (e.g., disturbance predictors). The rectangle represents 100% of the variation in Y. The total variation in Y is partitioned into four fractions. Fraction [b] is the intersection (or the shared variation between two sets of explanatory variables X and W) of the amounts of variation explained by linear models of X and W. Fraction [a] is the percentages of unique contribution of explanatory variables X and Fraction [c] is the unique contribution of explanatory variables W. Fraction [d] is the residual variation left unexplained by the canonical model. The Venn diagram is adapted from Legendre (1993).

4. RESULTS AND DISCUSSION

4.1. Species-area curve

The species-area curve was used to evaluate the adequacy of sample size in a community data set. The curve was plotted as cumulative species number versus sample plots. The sampling adequacy in terms of abundance was observed based on calculating the average Sorensen distance between the centroid of the subsample and the centroid of the whole sample. Species range in the sampling site collected was from 4.84 to 38 species (minimum and maximum) and the sampling plot range was from 1 to 90 plots. The Sorensen`s distance (dissimilarity) was from 0 to 0.63. The species accumulation curve elevated rapidly and become steepest in the early part of the collection as the common species were initially encountered, and then continued to rise very slowly and became shallower as all the rare species were also sampled (Figure 16).

In Figure 16, forty subplots yielded more than 30 species and with additional more subplots yielding relatively small increase in the number of species or no new species would likely be found with additional further sampling. This implied that the sample size used was adequate to address the existing species in the study sites. Similarly, the Sorensen's distance calculation between the centroid of the subsample and the centroid of the whole sample showed that 40 subplots yielded 30 species at Sorensen distance of less than 0.1 (< 10 %), which is quite small distance. The lower distance (Sorensen`s distance) between the centroid of the subsample and the centroid of the whole sample implied that subplots and the whole sample were similar and the more representative of the whole sample (McCune, 2002). The variability among

species at the lower sample size was higher (0.63) and lowers at higher sample size. As long as the sampling area was sufficiently homogeneous, all of the species was eventually sampled and the curve was flattened out at an asymptote that represented the true species richness for the assemblage.

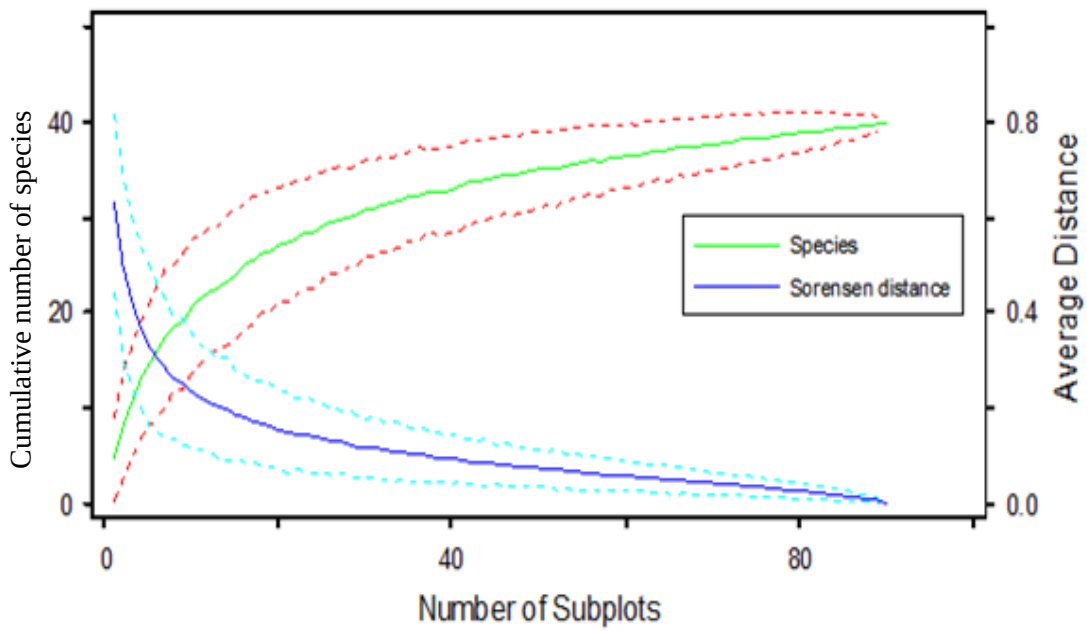


Figure 16. Species-area curve

Species-area curve (heavy green line, the middle line) used to assess sample adequacy based on repeated subsampling of a fixed sample (90 sample plots and 38 species). The dotted lines represent the +1 standard deviation. The distance curve (light blue) describes the average Sorenson distance between the subsamples and the whole sample, as a function of subsample size.

Table 4. List of species with scientific name, local name (*Afaan Oromoo*), family name and growth habit in Adaba-Dodola Afromontane forest

Scientific name	Local name	Family	Habit
Allophyllus abyssinicus (Hochst.) Radlk.	Abbaraa	Sapindaceae	Tree
Bersama abyssinica Fressen.	Koroqa/lolchiisaa	Melianiliaceae	Tree
Buddleja polystachya Fressen.	Bulchaanaa	Loganiaceae	Shrub
Carissa spinarum L.	Agamsa	Apocynaceae	Shrub
Discopodium pennlnervium Hochst.	Maraaroo	Solanaceae	Shrub
Dombeya torrida (J.F. Gmel) P. Bamps	Daannisa	Sterculiaceae	Tree
Dovyalis abyssinica (A. Rich.) Warb	Koshommii	Flacourtiacea	Tree
Ekebergia capensis Sparm.	Somboo/anoonoo	Meliaceae	Tree
Erica arborea L.	Saatoo	Ericaceae	Tree/Shrub
Galiniera saxifraga	Korraallaa	Rubiaceae	Tree
Gnidia glauca (Fresen.) Gilg	Diddiksaa	Thymelaceae	Shrub
Hagenia abyssinica (Bruce) J. Gmel.	Heexoo	Asteraceae	Tree
Hypericum revolutum Vahl	Garambaa	Guttiferae	Tree
Inula confertiflora A. Rich.	Haxaawwii	Asteraceae	Shrub
Juniperus procera L.	Hindheessa	Cupressaceae	Tree
Lobelia rhychnchopetalum		Lobeliaceae	Tree
Maesa lanceolata Forssk	Abbayyii	Myrsinaceae	Tree/Shrub
Maytenus arbutifolia (Hochst. ex A Rich.) Wilczt.	Qarxammee	Celastraceae	Tree
Maytenus undata (Thunb.) Blakelock	Kombolcha	Celastraceae	Shrub
Myrica salicifolia A.Rich.	Xonaa	Myricaceae	Tree
Myrsine africana L.	Qacama	Myrsinaceae	Shrub
Myrsine melanophloeos (L.) R. Br.	Tuullaa	Myrsinaceae	Tree
Nuxia congesta R. Br. ex fresen.	Bixxaannaa	Loganiaceae	Tree
Olea europaea subsp. Cuspidate (Wall. ex DC	Ejersa	Oleaceae	Tree
Olinia rochetiana A. Juss.	Gunaa / Daalachoo	OIiniaceae	Shrub
Osyris quadripartite Decn.	Waatoo	Santalaceae	Shrub
Podocarphus falcatus (Thunb.) Mirb	Birbirsa	Podocarpaceae	Tree
Prunus africana (Hook. f.) Kalkm.	Sukkee	Rosaceae	Tree
Pyschotria orophila		Acanthaceae	Tree
Rhamnus staddo A. Rich.	Qadiidaa	Rhamnaceae	Shrub
Rhus glutjnosa A. Rich.	Xaaxessaa	Anacardiaceae	Tree
Rosa abyssinica Lindley	Goraa luluffee	Rosaceae	Shrub
Rubus steudneri Schweinf	Goraa	Rosaceae	Liana
Schefflera myriantha (Bak.) Drake	Aaraa	Moraceae	Tree
Schefflera volkensii (Harms. ex.Engl.) Harms.	Aanshaa	Araliaceae	Tree
Scolopia theifolia Gilg.	Kokkolfaa	Flacourtiacea	Shrub
Sideroxylon oxyacantbum Baill.	Biitee/Faranqasa	Sapotaceae	Shrub
Vernonia rueppellii Sch. Bip. ex Walp.	Reejjii	Asteraceae	Shrub

4.2. Species composition and distribution

A total of 2087 individual woody plants of which 1482 (71%) trees, 415 (20 %) trees/ shrubs, 187 (9 %) shrubs and 3 (0.1 %) lianas belonging to 38 species and 30 families were recorded from all sites. Species such as *Juniperus procera*, *Erica arborea*, *Podocarpus falcatus*, *Hypericum revolutum* and *Maesa lanceolata* were the most five dominant species (Figure 17) comprising 554 (27 %), 438 (21 %), 319 (15%), 165 (8 %) and 152 (7 %) of the total individual plant species, respectively. Rosaceae was the most species-rich families comprising five species followed by Myrsinaceae and Asteraceae families containing three individual species each and Celasteraceae containing two species. 24 (80 %) families were represented by a single species in all study sites. Positive linear relationship ($r^2 = 0.77$; $p < 0.000$) was observed between species abundance and species frequency (Figure 18).

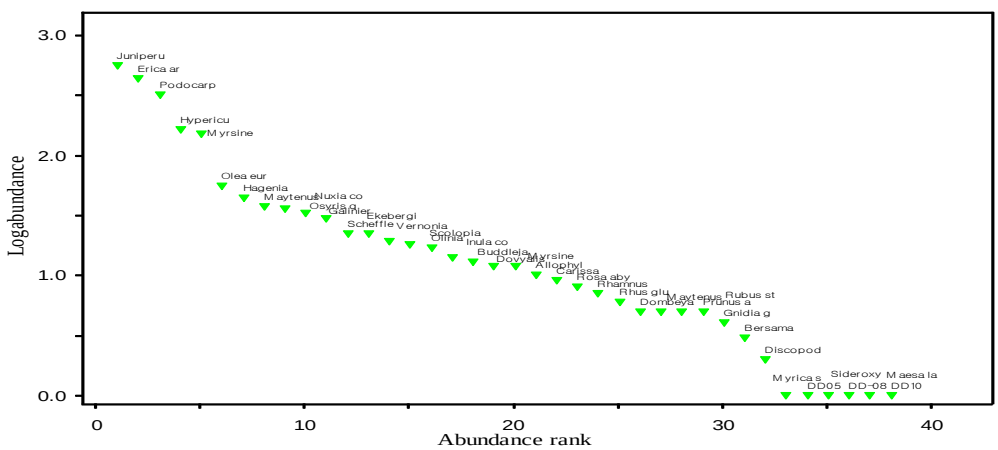


Figure 17. Dominance curve of species abundance rank (x-axis) against the logsum of abundance values for species (y-axis) in Adaba-Dodola Afromontane forest

Hypericum revolutum; Erica ar = Erica arborea; DD06= Schefflera myriantha; Hagenia= Hagenia abyssinica; Myrsine= Myrsine melanophloeos;Myrica s = Myrica salicifolia; Discopod = Discopodium pennlnervium; Grindia g = Gnidia glauca; Inula co= Inula confertiflora ; DD05= Lobelia rhychnchopetalum; Scolopia = Scolopia theifolia; Maesa la= Maesa lanceolate; Nuxia co = Nuxia congesta; Schefle v= Schefflera volkensii; Galin sax = Galiniera saxifrage; Osy qua = Osyris quadripartite; Myrsine a = Myrsine africana; Maytenus u = Maytenus undata; Ollinia= Olinia rochetiana; Rubus st = Rubus steudneri; Budelja = Buddleja polystachya; Dovylis= Dovyalis abyssinica; Maytenus= Maytenus arbutifolia; Vernonia = Vernonia rueppellii; Juniperu= Juniperus procera; DD10= Pyschotria orophila; Rhus glu= Rhus glutjnosa; Ekebergi= Ekebergia capensis; Sideroxy= Sideroxylon oxyacantbum; Podo carp = Podocarphus falcatus; Olea eur = Olea europaea; Bersama= Bersama abyssinica; Prunus a= Prunus africana; Rosa aby= Rosa abyssinica; Allophyll= Allophyllus abyssinicus; Rhamnus = Rhamnus staddo; Carrisa = Carissa spinarum

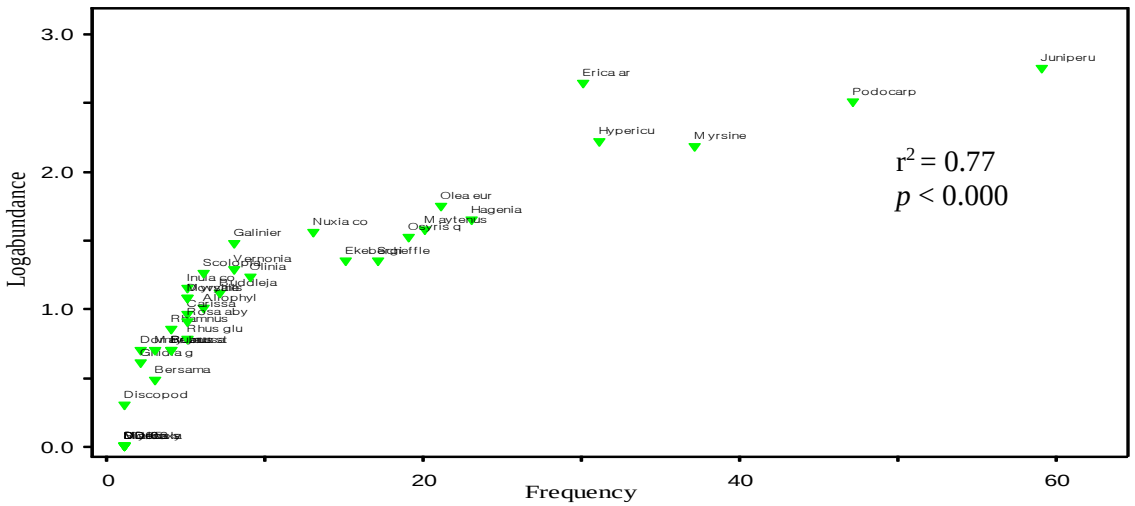


Figure 18. Relationship of species frequency (x-axis) and logsum of abundance values for species (y-axis) in Adaba-Dodola Afromontane forest.

Hypercu = Hypericum revolutum; Erica ar = Erica arborea; DD06= Schefflera myriantha; Hagenia= Hagenia abyssinica; Myrsine= Myrsine melanophloeos;Myrica s = Myrica salicifolia; Discopod = Discopodium pennlnervium; Grindia g = Gnidia glauca; Inula co= Inula confertiflora ; DD05= Lobelia rhychnchopetalum; Scolopia = Scolopia theifolia; Maesa la= Maesa lanceolate; Nuxia co = Nuxia congesta; Schefle v= Schefflera volkensii; Galin sax = Galiniera saxifrage; Osy qua = Osyris quadripartite; Myrsine a = Myrsine africana; Maytenus u = Maytenus undata; Ollinia= Olinia rochetiana; Rubus st = Rubus steudneri; Budelja = Buddleja polystachya; Dovylis= Dovyalis abyssinica; Maytenus= Maytenus arbutifolia; Vernonia = Vernonia rueppellii; Juniperu= Juniperus procera; DD10= Pyschotria orophila; Rhus glu= Rhus glutjnosa; Ekebergi= Ekebergia capensis; Sideroxy= Sideroxylon oxyacantbum; Podo carp = Podocarphus falcatus; Olea eur = Olea europaea; Bersama= Bersama abyssinica; Prunus a= Prunus africana; Rosa aby= Rosa abyssinica; Allophyll= Allophyllus abyssinicus; Rhamnus = Rhamnus staddo; Carrisa = Carissa spinarum

In the present study, majority of tree and shrub species exhibited a very narrow range of elevational distribution, though more proportion of shrubs had narrow range of distribution compared to trees (Figure 19). About 61% of the total tree species recorded in the study area exhibited narrow range of distribution whereas about 39% of them showed a wide distribution range. The tree species characterized with wide range of distribution in the study site include *Juniperus procera, Podocarphus falcatus, Myrsine melanophloeos, Erica arborea, Olea europaea, Hagenia abyssinica, Ekebergia capensis, Hypericum revolutum* and *Schefflera volkensii.* These species were distributed at least in two of the three elevation zones of the study sites considered.

Tree species such as *Allophyllus abyssinicus, Bersama abyssinica, Dombeya torrida, Dovyalis abyssinica, Galiniera saxifrage, Lobelia rhychnchopetalum, Maesa lanceolate, Maytenus arbutifolia, Myrica salicifolia, Prunus africana, Pyschotria orophila, Rhus glutjnosa, Schefflera myriantha* and *Nuxia congesta* had narrow range of distribution. The distribution range of these species was restricted to low and middle elevations, but their distribution range was not extended to the upper elevations (Figure 19). Distribution of most tree species was observed more concentrated in the middle elevation zones.

Majority of the distribution range of shrub species was restricted to elevation interval of 2560-3070-meter covering only the low and middle elevation zones of the study area. Only three shrub species namely, *Buddleja polystacya*, *Osyris quadripartite* and *Maytenus undata* had wide distribution range covering low to upper elevation zones. The shrub species that were characterized with narrow distribution range had shown two patterns of distribution. One pattern was that some species were aggregated only at low elevation areas (e.g. *Rhamnus staddo, Rosa abyssinica, Rubus steudneri, Scolopia theifolia* and *Carissa spinarum)* while the rest species were aggregated only around middle elevation areas (e.g. *Myrsine africana, Gnidia glauca, Inula confertiflora* and *Maesa lanceolate).* Generally, four patterns were observed in shrub distribution, the low elevation aggregation, the middle elevation aggregation, low and middle elevation distribution and the low to upper elevation distribution patterns. A total of 81% of shrub species had narrow range of distribution while 19% had wide elevational range of distribution.

There was no a species distributed over all elevations. The very narrow range of elevational distribution of species in this study site confirmed the general narrow distribution trend exhibited by various taxa along elevational gradients in the mountain

regions (Graham, 1990; Gaston, 1996; Cardelus *et al*., 2006). Jetz and Rahbek (2002) noted that many species have narrow elevation range beyond which they are unable to tolerate the climatic variations. Most species in the present study had either low abundance or very small range of distribution which were considered as rare taxa. Species which are less abundant (usually ≤ 5 individuals) and have narrow range of distribution are considered as rare taxa (Gaston, 1994). About 34 % of the Afromontane forest species observed in the present study had ≤ 5 individuals, i.e., rare taxa. According to Cowling (1990) and Goldblatt (1997), the distribution of species could be controlled by a dominating environmental, spatial or anthropogenic factors.

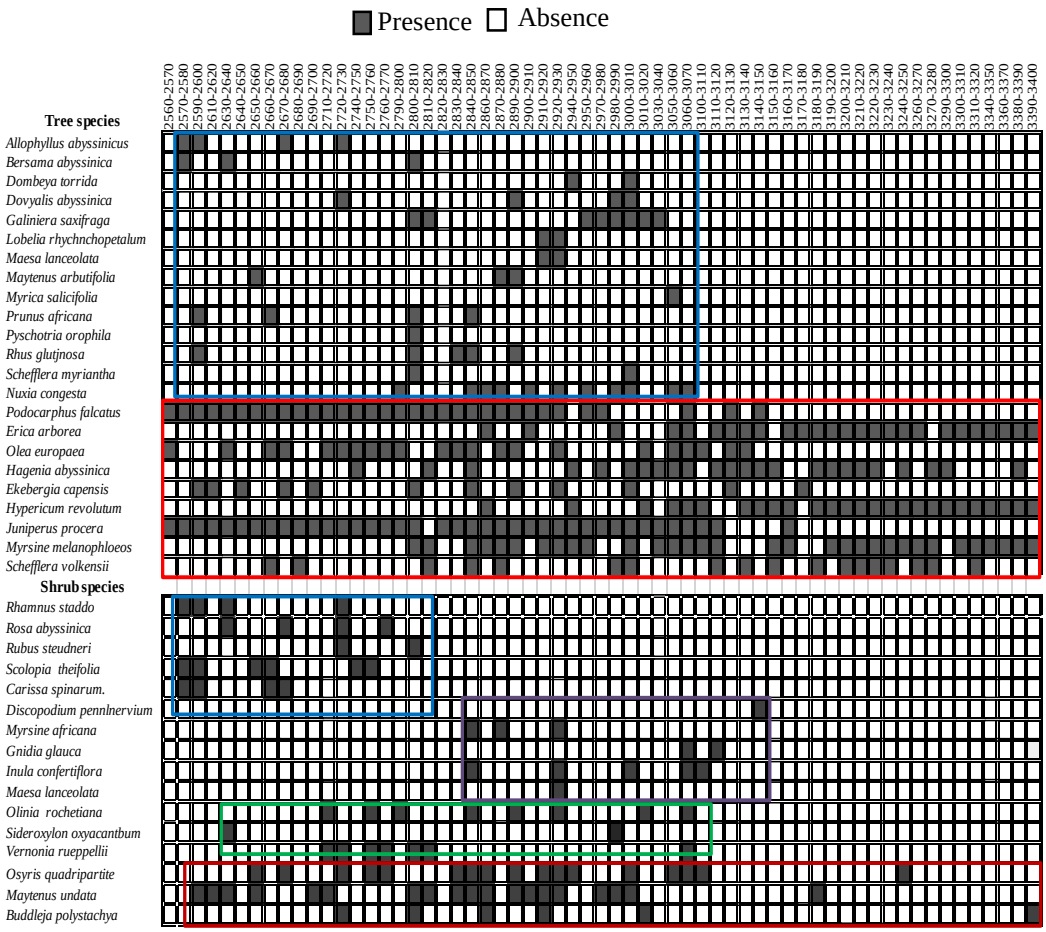


Figure 19. Distribution range of trees and shrub species along the elevation gradient

4.3. Community clustering and ordination analysis

The MRPP and the Indicator Species (IS) cluster analysis generated four groups of communities having similar floristic composition within a group (Figure 20 and Table 5). Groups of elevations with similar species composition were also consistently grouped together. Clustering the forest communities in four groups provided the maximum separation between groups, *T* and homogeneity within-groups, *A* (Table 6). There was a high species dissimilarity between the forest groups/

communities (overall Sorensen dissimilarity 79 %; T= -28.86, p= 0.000). Clustering the forests in four groups provided the most informative number of clusters with more homogeneity (A = 0.3428; p <0.0000). The four communities that contain 8-27 species include: remnants of low land forest community (*Podocarpus falcatus-Olea europea* forest community), middle elevation forest community (*Juniperus procera-Galiniera saxifraga* forest community), middle to upper elevation forests community (*Myrsine melanophloeos- Hagenia abyssinica* forest community) and the most upper elevation forest community (*Erica arborea-Hypercum revolutum* forest community*).*

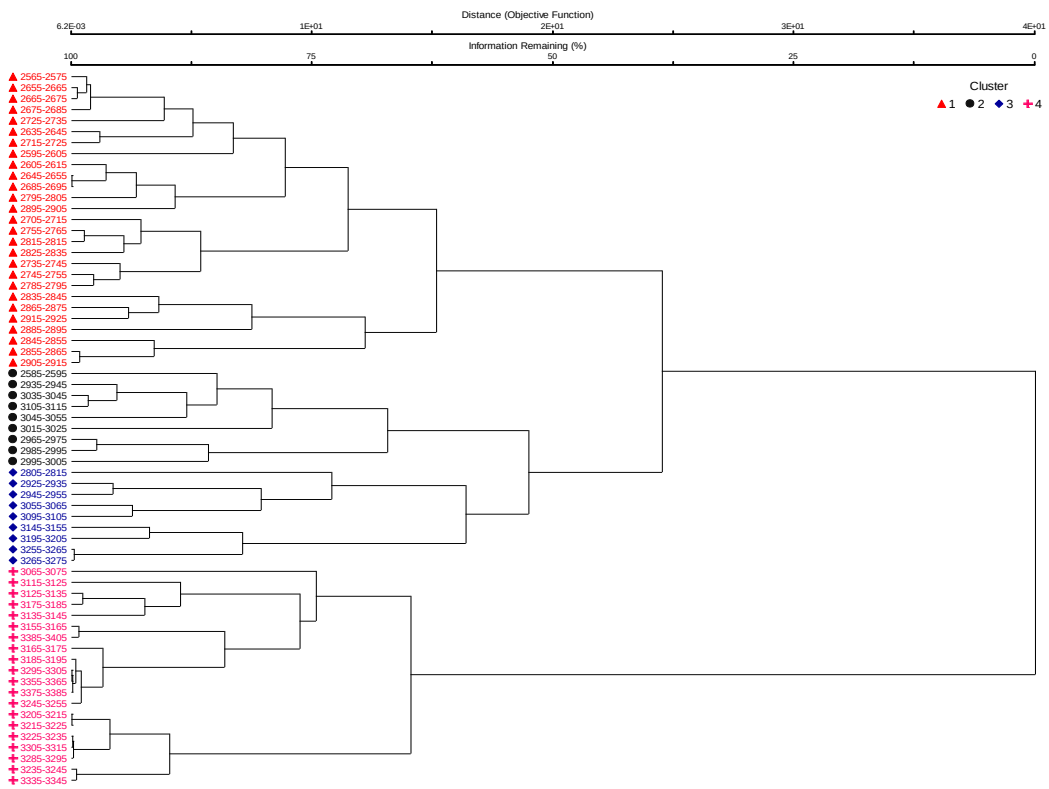


Figure 20. Dendrogram of the cluster analysis of 38 species

Dendrogram of the cluster analysis results of species abundance data of 38 species in 90 elevation units (65 elevations after pooled at 10 m elevation intervals) in Adaba-Dodola Afromontane forests. The grouping was at 59 - 67 % information remaining.

Table 5. Indicator values (% of perfect indication, based on combining the values for relative abundance & relative frequency) & Monte Carlo test for significance indicator valuesect

Species	*p- value*	IV	Family	Habit
Community I: *Podocarpus falcatus-Olea europea*:2565-2915m				
Allophyllus abyssinicus (Hochst.) Radlk.	0.2615	12	Sapindaceae	T
Bersama abyssinica Fressen.	0.1900	11	Melianiliaceae	T
Buddleja polystachya Fressen.	0.6503	7	Loganiaceae	S
Carissa spinarum L.	**0.0450**	19	Apocynaceae	S
Dovyalis abyssinica (A. Rich.) Warb	0.3017	6	Flacourtiacea	T
Ekebergia capensis Sparm.	0.0938	20	Meliaceae	T
Inula confertiflora A. Rich.	0.9120	1	Asteraceae	S
Juniperus procera L.	**0.0002**	39	Cupressaceae	T
Lobelia rhychnchopetalum	1.0000	4	Lobeliaceae	T
Maytenus arbutifolia (Hochst. ex A Rich.) Wilczt.	0.1908	11	Celastraceae	T
Maytenus undata (Thunb.) Blakelock	0.0764	25	Celastraceae	S
Myrsine africana L.	0.1440	15	Myrsinaceae	S
Myrsine melanophloeos (L.) R. Br.	**0.0002**	2	Myrsinaceae	T
Nuxia congesta R. Br. ex fresen.	0.3089	10	Loganiaceae	T
Olea europaea subsp. Cuspidate (Wall. ex DC)	**0.0002**	60	Oleaceae	T
Olinia rochetiana A. Juss.	0.1828	15	Oliniaceae	S
Osyris quadripartite Decn.	0.2987	15	Santalaceae	S
Podocarphus falcatus (Thunb.) Mirb	**0.0002**	80	Podocarpaceae	T
Prunus africana (Hook. f.) Kalkm.	0.1516	15	Rosaceae	T
Pyschotria orophila	1.0000	4	Acanthaceae	T
Rhamnus staddo A. Rich.	0.1326	15	Rhamnaceae	S
Rhus glutjnosa A. Rich.	**0.0454**	19	Anacardiaceae	T
Rosa abyssinica Lindley	0.1454	15	Rosaceae	S
Rubus steudneri Schweinf	0.4729	5	Rosaceae	L
Scolopia theifolia Gilg.	**0.0458**	22	Flacourtiacea	S
Sideroxylon oxyacantbum Baill.	1.0000	4	Sapotaceae	S
Vernonia rueppellii Sch. Bip. ex Walp.	0.1374	7	Asteraceae	S
Community II: *Juniperus procera-Galiniera saxifraga*: 2825-3115m				
Allophyllus abyssinicus (Hochst.) Radlk.	0.2615	4	Sapindaceae	T
Buddleja polystachya Fressen.	0.6503	5	Loganiaceae	S
Dombeya torrida (J.F. Gmel) P. Bamps	**0.0312**	22	Sterculiaceae	T
Dovyalis abyssinica (A. Rich.) Warb	0.3017	11	Flacourtiacea	T
Ekebergia capensis Sparm.	0.0938	10	Meliaceae	T
Erica arborea L.	**0.0002**	1	Ericaceae	T/S
Galiniera saxifraga	**0.0018**	42	Rubiaceae	T
Hagenia abyssinica (Bruce) J. Gmel.	**0.0210**	33	Asteraceae	T
Hypericum revolutum Vahl	**0.0066**	3	Guttiferae	T

Inula confertiflora A. Rich.	0.9120	4	Asteraceae	S
Juniperus procera L.	**0.0002**	45	Cupressaceae	T
Maytenus undata (Thunb.) Blakelock	0.0764	8	Celastraceae	S
Myrica salicifolia A.Rich.	0.2759	11	Myricaceae	T
Myrsine melanophloeos (L.) R. Br.	**0.0002**	11	Myrsinaceae	T
Nuxia congesta R. Br. ex fresen.	0.3089	14	Loganiaceae	T
Olea europaea subsp. Cuspidate (Wall. ex DC)	**0.0002**	1	Oleaceae	T
Olinia rochetiana A. Juss.	0.1828	3	OIiniaceae	S
Osyris quadripartite Decn.	0.2987	17	Santalaceae	S
Schefflera myriantha (Bak.) Drake	0.2747	11	Araliaceae	T
Schefflera volkensii (Harms. ex.Engl.)Harms.	0.1848	9	Araliaceae	T
Community III: *Myrsine melanophloeos-Hagenia abyssinica:* 2925-3275m				
Erica arborea L.	**0.0002**	1	Ericaceae	T/S
Galiniera saxifraga	**0.0018**	5	Rubiaceae	T
Hagenia abyssinica (Bruce) J. Gmel.	**0.0210**	12	Asteraceae	T
Hypericum revolutum Vahl	**0.0066**	28	Guttiferae	T
Inula confertiflora A. Rich.	0.9120	3	Asteraceae	S
Juniperus procera L.	**0.0002**	7	Cupressaceae	T
Maesa lanceolata Forssk	0.2759	11	Myrsinaceae	T/S
Maytenus undata (Thunb.) Blakelock	0.0764	5	Celastraceae	S
Myrsine melanophloeos (L.) R. Br.	**0.0002**	54	Myrsinaceae	T
Nuxia congesta R. Br. ex fresen.	0.3089	1	Loganiaceae	T
Osyris quadripartite Decn.	0.2987	1	Santalaceae	S
Podocarphus falcatus (Thunb.) Mirb	**0.0002**	6	Podocarpaceae	T
Rubus steudneri Schweinf	0.4729	6	Rosaceae	T
Schefflera volkensii (Harms. ex.Engl.) Harms.	0.1848	19	Araliaceae	T
Vernonia rueppellii Sch. Bip. ex Walp.	0.1374	14	Asteraceae	S
Community IV: *Erica arborea-Hypercum revolutum:*3065-3400 m				
Buddleja polystachya Fressen.	0.6503	1	Loganiaceae	S
Discopodium pennlnervium Hochst.	0.5789	5	Solanaceae	S
Erica arborea L.	**0.0002**	87	Ericaceae	T/S
Gnidia glauca (Fresen.) Gilg	0.1202	10	Thymelaceae	S
Hagenia abyssinica (Bruce) J. Gmel.	**0.0210**	11	Asteraceae	T
Hypericum revolutum Vahl	**0.0066**	41	Guttiferae	T
Inula confertiflora A. Rich.	0.9120	2	Asteraceae	S
Myrsine melanophloeos (L.) R. Br.	**0.0002**	12	Myrsinaceae	S
Nuxia congesta R. Br. ex fresen.	0.3089	1	Loganiaceae	T
Olinia rochetiana A. Juss.	0.1828	1	Oliniaceae	S
Schefflera volkensii (Harms. ex.Engl.)Harms.	0.1848	8	Araliaceae	T

Bold figures are indicator species with significant indicator value at $p < 0.05$ by Monte Carlo test; IV= indicator value

Table 6. Multiresponse permutation procedure (MRPP) pairwise comparison analysis for variations between communities

Pairwise comparison			***T***	***A***	***p***
Community I	vs.	Community II	-15.378	0.1125	<0.0000
Community I	vs.	Community III	-18.5525	0.1775	<0.0000
Community I	vs.	Community IV	-30.5821	0.3637	<0.0000
Community II	vs.	Community III	-6.98307	0.1392	<0.0000
Community II	vs.	Community IV	-17.0164	0.2917	<0.0000
Community III	vs.	Community IV	-13.8496	0.2028	<0.0000
Overall			-28.8631	0.3428	<0.0000

To test the significant differences between the groups of communities formed by the hierarchical clustering and indicator species analysis (ISA), multi-response permutation procedure (MRPP) was employed. In addition to a *p*-value, MRPP produced a statistic *A* that describes chance-corrected within-group heterogeneity. The test with a multi-response permutation procedure (MRPP) on differences in community composition between groups (clusters) and the Monte Carlo test indicated that there was highly significant variation in species composition between four groups of communities (T = -28.863; $p < 0.000$). The agreement within-group statistic A showed that there was high homogeneity within-groups (A= 0.3428; $p < 0.000$). The pairwise comparison of the group also showed that species composition differed significantly by vegetation group (T = -6.98307 to -30.5821; $p < 0.000$) (Table 6). This implied that all groups were responsible for the significant differences in the pattern of species composition between the clusters (groups). Environmental drivers such as climate, topographic heterogeneity, edaphic conditions and anthropogenic activities such as cutting, grazing and settlement contributed to the variation in forest communities across elevation. This study found that the most important environmental factor determining the distribution of tree community was elevation, similar to previous studies that tree species are more sensitive to elevation than soil fertility or

nutrient levels (Budke *et al.*, 2007; Zhang *et al.*, 2013; Takahashi and Murayama, 2014).

The names of the vegetation groups were assigned using the names of species with two high indicator values from indicator species analysis (Table 5). The four communities /vegetation type obtained by hierarchical cluster analysis were named after two of the most dominant and significant indicator species. The major characteristics of each community were summarized as follows:

***Podocarpus falcatus-Olea europea* forest community**

This community occurred between the elevational zones of 2565-2915m. This elevation ranges generally represented the low elevation zone of the study sites. This community consisted of 27 plots, 27 species and 884 individuals. The individual species of this vegetation community comprises 42% of the total individual species of the total community. The community had 7 indicator species with significant indicator values ($p < 0.05$). *Carissa spinarum, Juniperus procera, Myrsine melanophloeos, Olea europaea, Podocarphus falcatus, Rhus glutjnosa* and *Scolopia theifolia* were the species with high and significant indicator values of the community. The associated understory shrub species in this community type include *Buddleja polystachya, Inula confertiflora, Maytenus undata, Myrsine africana, Olinia rochetiana, Osyris quadripartite, Rhamnus staddo, Rosa abyssinica, Scolopia theifolia, Sideroxylon oxyacantbum* and *Vernonia rueppellii.* Significantly ($p < 0.05$), the highest pH was recorded in this forest community but the lowest OM (5.77 %) was recorded.

Juniperus procera-Galiniera saxifraga forest community

This community occupied the elevational zones between 2825-3115m. This elevation zone generally represented the middle elevation zone. The plant community was represented by 20 species and 346 individual species. This community has eight indicator species with significant indicator values at $p < 0.05$. The eight significant indicator species of the community include *Dombeya torrida, Erica arborea, Galiniera saxifraga, Hagenia abyssinica, Hypericum revolutum, Juniperus procera* and *Olea europaea.* This community was located on sloping terrains of 25-70% with mean slope angle of about 48% and occurred mainly on the upper slope position.

Myrsine melanophloeos-Hagenia abyssinica forest community

This community was located between 2925-3275m elevations. The community was represented by 15 species and 153 individuals. It was located in the mid to upper elevation of the study site. Seven of the indicator species of this forest community /group had significant values ($p < 0.05$) which include: *Erica arborea* ($p < 0.000$), *Galiniera saxifraga* ($p < 0.002$), *Hagenia abyssinica* ($p < 0.021$), *Hypericum revolutum* ($p < 0.007$), *Juniperus procera* ($p < 0.000$) and *Myrsine melanophloeos* ($p < 0.000$). *Myrsine melanophloeos* and *Hypericum revolutum* were exclusively the dominant canopy tree species in this vegetation community comprising more than 65% of the total tree population. *Inula confertiflora, Maesa lanceolate, Maytenus undata, Nuxia congesta, Osyris quadripartite, and Rubus steudneri* were the rare species in this vegetation.

Erica arborea-Hypercum revolutum forest community

This community was located at upper elevation of the study site at the elevation of 3065-3400 m. It was represented by 11 species and 648 individuals (200 trees, 17 shrubs and 431 trees / shrubs). It was characterized with four indicator species with significant indicator values ($p < 0.05$). About 85 % of the total individuals in this community were contributed by *Erica arborea* and *Hypercicum revolutum* only. Based on the soil nutrient rating in the country (Tekalign, 1991), the soil of *Erica arborea-Hypercum revolutum* forest community was categorized as strongly acidic (pH = 5.1) and high OM content (8.35 %). The high OM in this community might be related to the slow OM decomposition rate due to cool temperature. Zhang *et al*. (2010) also reported similar result that soil OM increased by increasing altitude probably due to lower soil temperatures, which would retard the decomposition of litter. High TN was also found in *Erica arborea- Hypercum revolutum forest* community that might be attributed to accumulation of TN due to low soil temperature (Ji, 1996).

According to nutrients ratings in Ethiopia by Tekalign (1991), the total N was very high in all vegetation communities as compared to the national rate and was significantly high in upper elevation zone. There was low available Phosphorus (AvP) in all forest communities though the value was not significantly ($p > 0.05$) different between the forest communities (Table 7). In all vegetation communities, the level of OM was very high as per the soil nutrient rating of the country made by Tekalign (1991).

The species composition of the four vegetation types observed in the present study was compatible with that of the other Afromontane forest of Ethiopia. Most of

the significant indicator species in the present study were the characteristic features of Afromontane forests identified by Friis (1992) in other study sites.

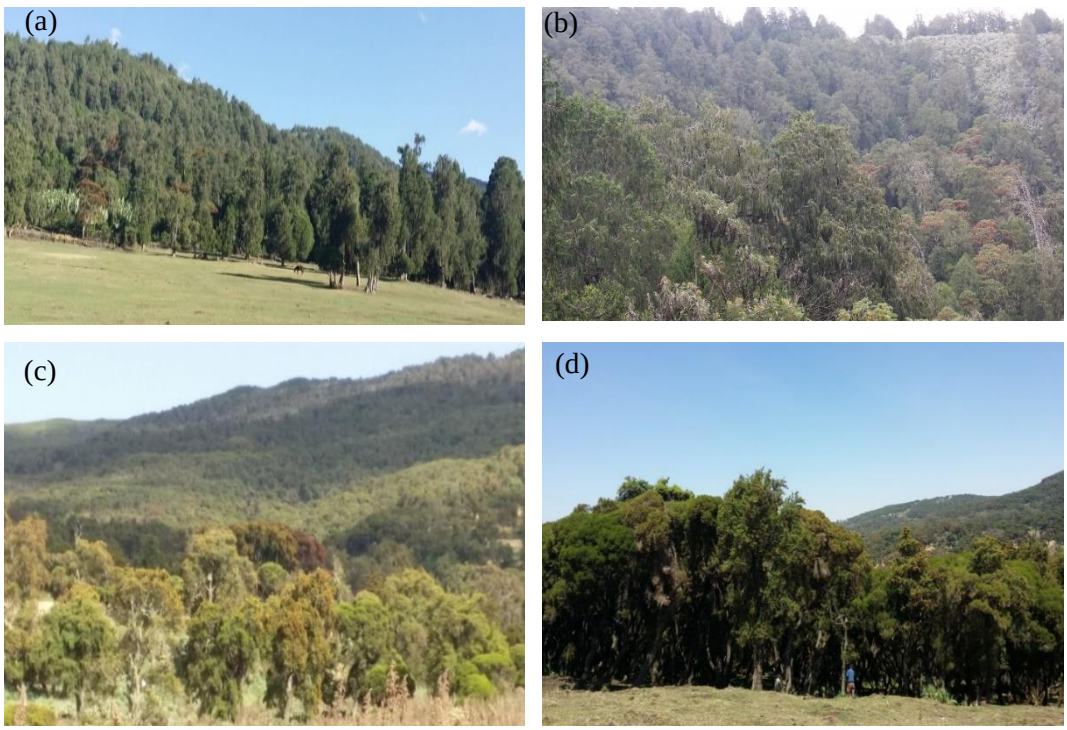


Figure 21. Views of dominant vegetation in community clusters (a) *Podocarpus falcatus-Olea europea* vegetation: 2565-2915m; (b) *Juniperus procera-Galiniera saxifraga* forest: 2825-3115m; (c) & (d) *Erica arborea-Hypercum revolutum* vegetation: 3065-3400 m (date of photo: February 5-11, 2016)

Table 7 . Characteristics of studied community in Adaba-Dodola Afromontane forest, Ethiopia

	Forest communities				
Parameters	I	II	III	IV	Mean
No. plots	27	10	8	20	65*
Elevation (m)	2742^{a}	2967^{b}	3098^{c}	3256^{d}	2979
Aspect (o)	187.33±100^{a}	217±112^{a}	214.25±116^{a}	227.8±91^{a}	207.66±100
Slope (%)	38.40±13.59^{b}	49.60±13.17^{a}	42.63±13.51^{ab}	34.90±9.34^{b}	39.57±13
MC (%)	0.39±0.07^{c}	0.51±0.20^{b}	0.42±0.07^{c}	0.65±0.09^{a}	0.49±0.15
BD (g/m^{3})	0.81±1.00^{a}	0.50±0.15^{c}	0.61±0.12^{b}	0.64±0.12^{b}	0.67±0.57
TN (%)	0.42±0.14^{b}	0.43±0.10^{b}	0.49±0.14^{b}	0.63±0.12^{a}	0.49±0.16
AvP(ppm)	6.68±5.86^{ns}	7.19±4.29^{ns}	7.03±6.43^{ns}	4.74±2.08^{ns}	6.63±5.46
OM (%)	5.77±1.81^{b}	7.59±2.93^{ab}	7.07±2.03^{ab}	8.35±2.2 3^{a}	7.48±2.57
EC (mmho/cm)	0.15±0.08^{b}	0.25±0.12^{a}	0.20±0.10^{ab}	0.29±0.10^{a}	0.22±0.11
pH (H_2O)	6.35±0.61^{a}	6.23±0.72^{b}	5.88±0.68^{b}	5.13±0.39^{c}	5.91±0.78
STL (m)	460.63±93^{b}	1372±434.9^{a}	1306±42.84^{a}	429±95.32^{b}	693±81.89
Agri (m)	153±46.84^{a}	482±33.21^{b}	130±52.97^{a}	206±54.19^{a}	217±41.80
Road (m)	270±42.05^{a}	1046±29.91^{b}	1331±44.35^{b}	299±48.84^{a}	529±71.79
CO (%)	60.00±6.48^{ns}	60.5±10.93^{ns}	62.75±9.60^{ns}	59.20±6.49^{ns}	60.18±7.59
Cutting	13.35±18.33^{a}	2.50±3.03^{c}	6.00±5.24^{bc}	8.78±7.65^{b}	8.88±11.89
Grazing	1.33±1.00^{a}	0.25±0.55^{b}	0.50±0.76^{b}	1.30±1.64^{a}	0.89±1.09
Species richness	6.67±2.22^{b}	7.70±3.47^{a}	4.50±0.93^{c}	3.65±1.35^{c}	5.63±2.61
Evenness	0.75±0.14^{b}	0.93±0.02^{a}	0.94±0.03^{a}	0.64±0.25^{c}	0.77±0.20
Shannon diversity	1.40±0.38^{b}	1.83±0.45^{a}	1.39±0.19^{b}	0.81±0.36^{c}	1.28±0.50
Simpsons	0.67±0.14^{b}	0.80±0.08^{a}	0.73±0.05^{b}	0.45±0.19^{c}	0.63±0.19

Values indicated with letter of different superscript across a row are significantly different at 0.05. Agri = agricultural distance to forest; STL = settlement distance to forest; Road= road distance to forest; CO= canopy openness; MC= soil moisture; BD= bulk density; TN= total nitrogen; AvP= available phosphorus; OM= organic matter; EC= electrical conductivity; S= species richness; E= evenness; H= Shannon diversity; D= Simpson index; I= *Podocarpus falcatus-Olea europea* community; II= *Juniperus procera-Galiniera saxifraga* community; II = *Myrsine melanophloeos-Hagenia abyssinica* community; II = *Erica arborea-Hypercum revolutum* Community).* Notice that the total number of plots is 90, but since the cluster was based on the elevation interval, the total clustered plots became 65. Cutting is expressed in terms of density of tree and shrub stumps; grazing is expressed in terms of the density of grazed (browsed) saplings and seedlings.

4.4. Species dispersion patterns

Species dispersion patterns show the spatial relationship between species within a forest community. Species found in the Adaba-Dodola forest showed varying patterns of dispersion. The species were dispersed in the two basic patterns: random (individuals spaced at unpredictable distances from each other) and clumped /aggregated (individuals grouped together). The number of species showing dispersion patterns at each of the four forest community was given in Table 8. An analysis of

dispersion pattern indicated that more species had clumped distribution pattern in all forest communities. 33–92 % species in the community had clumped dispersion pattern. Relatively, forest communities of *Juniperus procera-Galiniera saxifraga* and *Myrsine melanophloeos-Hagenia abyssinica* had less clumped dispersion pattern (33 % and 64 %) than *Podocarpus falcatus-Olea europea* community and *Erica arborea-Hypercum revolutum forest* communities (68 % and 92 %). This means the forest communities found at the two extreme elevation levels had highly clumped or aggregated species than the forest communities at the middle elevations. This might have been related to human disturbance at low elevation and climatic factors at high elevation zones. There was no uniform species dispersion pattern in any forest community. Of the total analyzed species, 13 (34 %) of them showed a changing nature in dispersion from one community to the other community along the elevation gradient. 7 (54 %) of these species changed from clumped to random dispersion (e.g. *Dovyalis abyssinica*, *Podocarphus falcatus* and *Rubus steudneri,* etc.*).* Similarly, 6 (46 %) of them were changed from random to clumped dispersion (eg. *Hagenia abyssinica*, *Ekebergia capensis*, *Hypericum revolutum, Osyris quadripartite,* etc.).

Hubbell *et al*. (1999) reported that the dispersal limitation is an important ecological factor for controlling species distribution pattern and a connection between biotic and abiotic ecological factors. The species-aggregation relationship predicts that spatial aggregation of individuals within species results in lower species richness (Sagar *et al*., 2008). According to Odum (1971), the clumped distribution is common in nature, while random distribution is found only in uniform environments. The clumping of individuals of a species may be due to insufficient mode of seed dispersal (Richards, 1996). On the other hand, Armesto *et al.* (1986) stated that clumping occurs when death of trees creates a large gap encouraging recruitment and growth of

numerous saplings. Clumped dispersion patterns of species with high abundance (e.g., *J. procea* and *P. falactus*) in the current study may be related to their profound coppicing ability (Sagar *et al*., 2003). Connell (1978) suggested that the uniform dispersion pattern of species in tropical forests largely enables the maintenance of high levels of diversity. The changes in the dispersion patterns may reflect the reactions of species to disturbance as well as to changes in the habitat conditions (Sagar *et al*., 2003). Dispersion patterns of species can also change with changes in disturbance intensities, reflecting their responses to disturbance (Sagar *et al*., 2003) and competition (Rozas and Fernandez, 2000).

He *et al*. (1997) also stated that as succession proceeds with some intervention, population spatial patterns shift from highly clumped to more random or uniform distributions. Generally, the combined effects of many biotic and abiotic disturbance factors affect species' distribution patterns (He *et al*., 1997; Rozas and Fernandez, 2000).

Table 8. Species distribution and dispersion pattern in four forest communities

	Community I		Community II		Community III		Community IV	
Species	V/M	Dispersion	V/M	Dispersion	V/M	Dispersion	V/M	Dispersion
Allophyllus abyssinicus	2	C						
Bersama abyssinica	1	R						
Buddleja polystachya	3	C	2	C				
Carissa spinarum	2	C						
Discopodium pennlnervium							2	C
Dombeya torrida			2	C				
Dovyalis abyssinica	5	C	1	R				
Ekebergia capensis	1	R	3	C				
Erica arborea			2	C	1	R	10	C
Galiniera saxifraga	2	C	5	C	2	C		
Gnidia glauca							2	C
Hagenia abyssinica	1	R	3	C	2	C	3	C
Hypericum revolutum			1	R	8	C	7	C
Inula confertiflora			3	C	1	R	7	C
Juniperus procera	9	C	5	C	6	C	2	C
L. rhychnchopetalum			1	R				
Maesa lanceolata					1	R		
Maytenus arbutifolia	2	C						
Maytenus undata	2	C	1	R	1	R		
Myrica salicifolia			1	R				
Myrsine africana	2	C	4	C				
Myrsine melanophloeos	4	C	4	C	1	R	5	C
Nuxia congesta	3	C	4	C	1	R	4	C
Olea europaea	2	C	8	C				
Olinia rochetiana	3	C	2	C				
Osyris quadripartite	1	R	3	C	1	R	2	C
Podocarphus falcatus	8	C	11	C	1	R		
Prunus africana	1	R	1	R				
Pyschotria orophila	1	R						
Rhamnus staddo	2	C						
Rhus glutjnosa	1	R	1	R				
Rosa abyssinica	3	C						
Rubus steudneri	2	C	1	R	1	R		
Schefflera myriantha			1	R				
Schefflera volkensii	1	R	1	R	1	R	2	C
Scolopia theifolia	4	C						
Sideroxylon oxyacantbum	1	R						
Vernonia rueppellii	3	C			2	C		
Dispersion pattern								
Clumped (C)	19 (68 %)		16 (64%)		5 (33%)		11(92%)	
Random (R)	9 (32%)		9 (36%)		10 (67%)		1 (8%)	
Uniform (U)	0 %		0%		0%		0%	

Random dispersion (*R*) occurred when *Variance-to-mean ratio* (*V/m)* =1; a uniform dispersion (*U*) for *v/m* ratio < 1 and clumped dispersion (*C*) for *v/m* ratio >1.

4.5. Alpha (α), beta (β) and gamma (γ) diversity in forest communities

The α-diversity (mean species richness) ranged from 3.65 in community IV to 7.70 in community II with overall mean richness of 5.63 (Table 9). Alpha diversity was significantly ($p< 0.005$) highest in community II (7.7) and lowest in community IV (3.65). Shannon diversity indices ranged from 0.81 to 1.83, with significantly ($p< 0.005$) the highest value in community II (the middle elevation zone) and the lowest in community IV (the upper elevation zone). There was highest concentration dominance (Simpson`s index, D) or species abundance in community II.

In this study, the highest and the lowest Whittaker beta diversity (β_w) were recorded in community I (2.73) and community II (2.25), respectively (Table 9). In other words, there was high species composition change (species turnover) within community I along the elevation gradients. All forest communities had intermediate beta diversity (β_w) because as a rule of thumb, $\beta_w < 1$ is considered as low beta diversity, while $\beta_w > 5$ can be considered high (McCune, 2002). However, the overall beta diversity (β_w) in the Adaba-Dodola forest was high (i.e., $\beta_w = 5.75$, $\gamma = 38$; $\alpha = 5.63$).

Table 9. ANOVA of diversity indices among communities in Adaba Dododola Afromontane forests, Ethiopia

Diversity characteristics	Forest community				
	I	II	III	IV	Overall
Alpha α-diversity	6.67±2.22[b]	7.70±3.47[a]	4.50±0.93[c]	3.65±1.35[c]	5.63±2.61
Shannon diversity, *H`*	1.40±0.38[b]	1.83±0.45[a]	1.39±0.19[b]	0.81±0.36[c]	1.28±0.50
Evenness index, *E*	0.75±0.14[b]	0.93±0.02[a]	0.94±0.03[a]	0.64±0.25[c]	0.77±0.20
Simpson`s index, *D*'	0.67±0.14[b]	0.80±0.08[a]	0.73±0.05[b]	0.45±0.19[c]	0.63±0.19
Gamma γ-diversity	27	25	15	13	38
Whittaker β-diversity (β_w)	3.03	2.25	2.33	2.51	5.75
Total individual species	884	346	209	648	2087
SR : Individual ratio	0.03	0.07	0.07	0.02	0.02

Based on Whittaker (1972): Alpha diversity was calculated here as the average species richness, Whittaker beta diversity (β_w) is a measure of turnover in the data which was calculated with the ratio of gamma diversity to alpha diversity minus one ($\gamma / \alpha - 1$). Gamma diversity is estimated as the total number of species across all plots. SR= Total species richness (γ-diversity). Means with letters different superscript are significantly different at 0.05 across the row

4.6. Floristic similarities

Sorensen's similarity coefficient indicated the highest floristic similarity between community I and community II (0.65) followed by community III and community IV (0.64) (Table 10). This may be due to the proximity of communities to each other that attributed to similar adaptation mechanisms and requirements for species occurring in those communities. The lowest similarity was observed between community I and community IV (0.40) that was found at the distant location and long elevational range from each other. An overall similarity coefficient was observed to be 0.21, which was a low floristic similarity between communities in Adaba-Dodola forest. The relationship between beta diversity (turnover) and Sorensen's similarity coefficient showed an inverse relationship. Highest beta diversity (species turn over) was observed in pairs of community I and community IV that occupied the two extreme elevation pairs where a 60 % species change was estimated (Table 10).

Table 10. Species turnover and Sorensen's similarity coefficient in clustered communities

Parameters	I vs II	I vs III	I vs IV	II vs III	II vs IV	III vs IV
Species turnover (β_T)	0.35	0.52	0.60	0.40	0.47	0.36
No. of common species	17(45)	10(26)	8(21)	12(32)	10(26)	9(24)
Sorensen`s similarity index	0.65	0.48	0.40	0.60	0.53	0.64
Overall Sorensen`s similarity index: 0.21						

Values in the bracket are the percent of common species to the pair of community. I-IV= forest communities

4.7. Forest stand structure

Vegetation stands structure refers to the numerical distribution of different sized individuals that form a community (Muller-Dombois and Ellenberg, 1974). In the investigation of the structure of woody plant species, density, basal area and frequencies were considered. The growth stage of trees as seedlings, saplings and mature trees in a population can permit or deny the chance of rapid recovery of the forest after disturbance (Muller-Dombois and Ellenberg, 1974).

4.7.1. Density

The mean density of woody plants (DBH $\geq$ 2cm) in the study site was 579.72 stems ha^{-1} of which, 261stems ha^{-1}, 96 stems ha^{-1}, 43 stems ha^{-1} and 180 stems ha^{-1} were contributed by forest community I, II, III and IV, respectively. Except in community IV, in which the tree/shrub (i.e., *Erica arborea*) life form was more abundant (120 stems ha^{-1}; 67%), more density was recorded from tree life forms in all communities (Table12). In community I, tree life form constituted 224 stems ha^{-1} (86%), shrubs 36 stems ha^{-1} (14 %) and lianas 0.83 stems ha^{-1} (0.32%). In community II, the total density of tree life form was 83 stems ha^{-1} (86 %), shrubs 12 stems ha^{-}

^{1}(12 %), trees/shrubs 1 stems ha^{-1} (1.2 %) and lianas 0.28 stems ha^{-1}(0.29 %). Similarly, in community III, the total density of tree life form was 39 stems ha^{-1} (93%), shrubs 1.4 stems ha^{-1} (3.3 %), trees /shrubs 1.1 stems ha^{-1} (2.6%), lianas 0.28 stems ha^{-1} (0.65%). In community IV, the total density of tree life form was 56 stems ha^{-1} (31%), shrubs 4.7 stems ha^{-1} (2.6 %) and trees/shrubs 120 stems ha^{-1} (67%). The highest density of tree/shrub life form in community IV, which was located in the upper vegetation zone of the study area, was due to the exclusive dominance of *Erica arborea* species.

Table 11. General Linear Model (Mean ± SE) of woody plant structural parameters in forest communities

Variables[a]	Community			
	I	II	III	IV
DBH (cm)	26.31±2.38^{b}	31.41±3.91^{ab}	36.27±4.37^{a}	29.19±2.76^{ab}
Height (m)	10.23±0.55^{a}	11.43±0.91^{a}	10.65±1.01^{a}	8.38±0.64^{b}
Canopy cover (%)	6.72±0.63^{a}	7.23±1.04^{a}	8.59±1.16^{a}	6.08±0.74^{b}
Canopy openness (%)	60.0±6.48^{ns}	60.5±10.93^{ns}	62.75±9.60^{ns}	59.20±6.49^{ns}

Means with different let of superscript across rows are significantly different; [a]values for each variable indicate the mean values in a plot for each community

Table 12. Density (stem/ha) and density proportion (%) of life forms in each forest community

Life form	I		II		III		IV	
	Density	%	Density	%	Density	%	Density	%
Tree	224.44	85.99	82.78	86.13	39.72	93.46	55.56	30.86
Shrub	35.83	13.73	11.94	12.43	1.39	3.27	4.72	2.62
Tree/shrub	0	0	1.11	1.16	1.11	2.61	119.72	66.51
Liana	0.83	0.32	0.28	0.29	0.28	0.65	0	0
Total	261	100	96	100	43	100	180	100

The top five woody species with the highest density in community I were *Juniperus procera* (104.7 stems ha^{-1}), *Podocarpus falcatus* (82.6 stems ha^{-1}), *Olea europaea* (10 stems ha^{-1}) and *Maytenus undata* (8.61 stems ha^{-1}) and *Myrsine*

melanophloeos (6.4 stems ha^{-1}) (Figure 22). These species were not only the most abundant but also were the most frequent in the study area. Likewise, the top five woody species with the highest density in community II were *Juniperus procera* (40.83 stems ha^{-1}), *Myrsine melanophloeos* (7.22 stems ha^{-1}), *Galiniera saxifraga* (6.67 stems ha^{-1}) and *Podocarpus falcatus* (5.83 stems ha^{-1}) and *Olea europaea* (5.28 stems ha^{-1}). In the community III, the top five species with high density were *Myrsine melanophloeos* (16.11 stems ha^{-1}), *Hypericum revolutum* (11.67 stems ha^{-1}) and *Juniperus procera* (7.78 stems ha^{-1}) *Hagenia abyssinica* (1.67 stems ha^{-1}) and *Schefflera volkensii* (1.11 stems ha^{-1}). *Erica arborea* (119.72 stems ha^{-1}), *Hypercum revolutum* (33.06 stems ha^{-1}), *Myrsine melanophloeos* (12.50 stems ha^{-1}), *Hagenia abyssinica* (5.28 stems ha^{-1}) and *Schefflera volkensii* (3.06 stems ha^{-1}) were the most dominant in community IV.

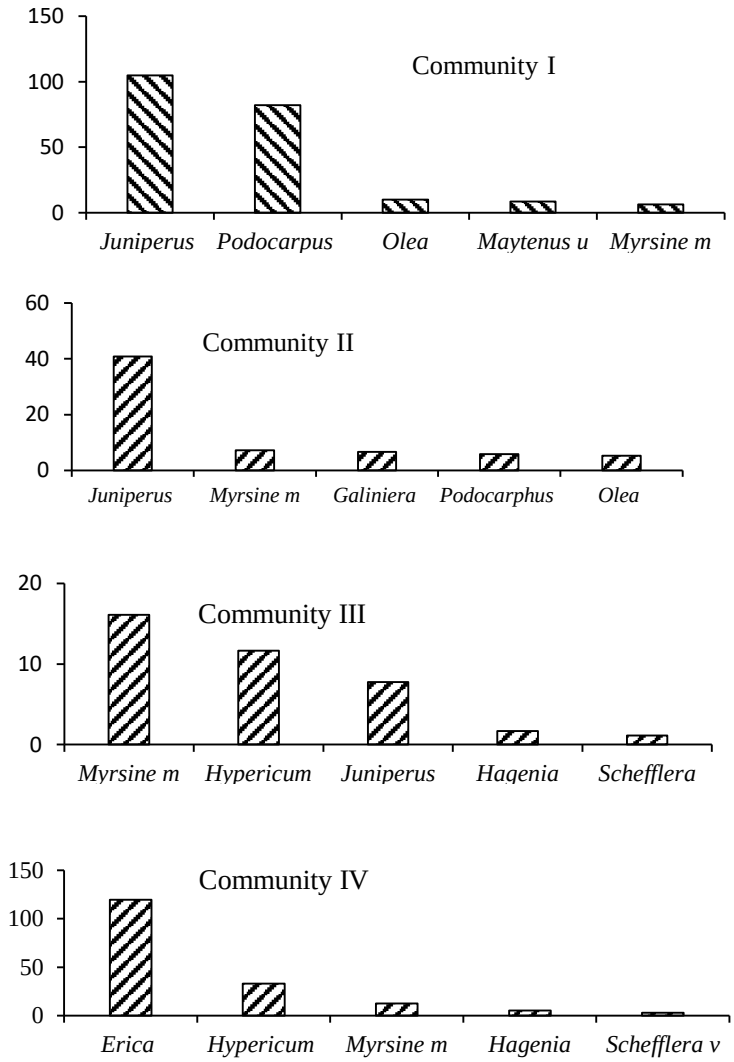


Figure 22. Top five woody species with high density in each of the four communities

Juniperus= Juniperus procera; Podocarpus = Podocatpus falcatus; Myrsine m = Myrsine melanophloeos, Olea = Olea eropaea, Maytenus u = Maytenus undata, Galiniera = Galiniera saxifrage; Hypercum = Hypercum revolutum; Hagenia= Hagenia abyssinica; Scheffleria = Scheffleria volkensii

4.7.2. Forest size class distribution based on density ratio (*a*/*b*)

According to Grubb *et al*. (1963), the ratio of density of individuals with DBH > 10 cm (10.01 cm to 20 cm) to DBH > 20 cm was taken as the measure of size class distribution in a forest. Accordingly, the density of tree species in Adaba-Dodola forest with DBH > 10 cm and > 20 cm were 134.7 and 284.1 stems ha^{-1}, respectively (Table 13). The density of woody species with (DBH > 10 cm) greater than 600 individual ha^{-1} is normal for virgin rain forest in Africa (Richards, 1966 cited in Lamprecht, 1989). However, very low density (DBH > 10 cm; 134.7 stems ha^{-1}) was recorded in Adaba-Dodola forest compared to the normal density of African rain forest.

The ratio of tree density with DBH > 10 cm to DBH > 20 cm in Adaba-Dodola was 0.5. This value was compared with that of seven other Afromontane forests in Ethiopia (Table 13). Adaba-Dodola forest ranked last (8^{th}) in tree density for individuals with DBH > 10 cm but it was ranked 3^{rd} in density of individual trees with DBH > 20 cm. The density ratio (*a/b*) of Adaba-Dodola forest was the smallest from the compared Afromontane forests in Ethiopia. This showed that the proportion of medium sized and large-sized individuals much differ in Adaba-Dodola Afromontane forest indicating that the large-sized (may be old-aged) trees were predominant in Adaba-Dodola Afromontane forest. Comparatively, Masha-Andaracha, Menna-Angetu and Jibat Afromontane forests had 4-5 times more *a/b* ratio values than Adaba-Dodola forest indicating that there was more predominance of trees in the lower DBH class in these forests than in Adaba-Dodola forest.

Table 13. Tree density (stem/ ha) comparison of Adaba-Dodola Afromontane forest with other Afromontane forests in Ethiopia based on density ratio (a/b)

Afromontane forests	DBH class				Ratio
	DBH >10 cm	Rank	DBH >20 cm	Rank	*a/b*
Menna-Angetu[1]	292.6	7	139.8	8	2.1
Jibat[2]	565.0	1	287.0	2	2.0
Mash-	384.7	4	160.5	7	2.4
Alata-Bolale[4]	365.0	5	219.0	5	1.7
Bibita	500.5	3	265.6	4	1.9
Jima[6]	335.0	6	184.0	6	1.8
Sese[7]	513.7	2	412.7	1	1.2
Adaba-Dodola	134.7	8	284.1	3	0.5

Reference: [1]Ermias *et al.* (2008), [2]Tamrat (1993), [3]Kumelachew and Taye (2003), [4]Woldeyohannes (2008), [5]Dereje (2007), [6]Fufa (2008), [7]Shiferaw (2010)

4.7.3. Basal area

Basal area (BA) provides a better measure of the relative importance of tree species than simple counts. Species with the largest contribution in BA can be considered as the most important species in a forest (Bekele, 1993). Basal area per hectare could be used as an indicator of the level of degradation or status of standing stock. If basal area is declining, it can be safely concluded that the forest is degrading.

There was no significant difference between the forest communities in terms of basal area. However, the highest mean basal area was recorded from *Juniperus procera-Galiniera saxifraga* forest community (C-II) (Table 14). The least mean basal area was recorded in *Erica arborea-Hypercum revolutum* forest community (C-IV). *Juniperus procera* (13.70 m^2/ha) and *Podocarpus falcatus (*8.95 m^2/ha*)* contributed the largest total basal area in *Podocarpus falcatus-Olea europea* forest community while *Juniperus procera* (7.53 m^2/ ha*)* and *Hagenia abyssinica* (1.68 m^2/ ha) contributed the largest basal area in *Juniperus procera-Galiniera saxifraga* forest community. Similarly, *Juniperus procera* (3.07 m^2/ ha) and *Hagenia abyssinica* (1.86

m^2/ ha) contributed the largest share in *Myrsine melanophloeos-Hagenia abyssinica* fiorest community and *Erica arborea* (9.43 m^2/ ha) and *Hagenia abyssinica (*3.18 m^2/ ha) in *Erica arborea-Hypercum revolutum* forest community. More basal area was contributed by very few individual trees that attained greater diameter at breast height. Majority (84.4%) of the total basal area was accounted by four dominant species: *Juniperus procera* (40.9 %), *Erica arborea* (16.6 %), *Podocarpus falcatus* (15.6 %) and *Hagenia abyssinica* (11.4 %).

The total basal area in Adaba-Dodola Afromontane forest (59.74 m^2ha^{-1}) was greater than the basal area of some Afromontane forests in Ethiopia such as Aleta Bolale, Jibat, Bonga, Menagesha, Jimma and Chilimo forests that have basal area (Table 14). However, the basal area of current study area was lower than that of Wof washa (101.8 m^2 ha^{-1}), Mena-Angetu (94.22 m^2 ha^{-1}), Sese (88.62 m^2 ha^{-1}), Masha Andasa (81.90 m^2 ha^{-1}) and Gura-Farda (69.90 m^2 ha^{-1}) Afromontane forests in Ethiopia. The normal value of basal area for virgin tropical rain forests in Africa was estimated to be 23 to 37 m^2 ha^{-1} (Dawkins, 1959 as cited in Lamprecht, 1989). Based on this result, the basal area for Adaba-Dodola forest was high. The volume increment of natural tropical high-forest and limitations on its improvements.

Table 14. Comparison of Adaba-Dodola forest with other 12 Afromontane forests in Ethiopia in terms of basal area.

Forest	Basal area m^2ha^{-1}	Reference
Wof washa	101.80	Tamerat (1994)
Menna-Angetu	94.22	Ermias Lulekal (2005)
Sese	88.62	Shiferaw (2010)
Masha Andasa	81.90	Kumelachew and Taye (2003)
Gura-Farda	69.90	Dereje (2007)
Adaba-Dodola*	59.74	Present study
Aleta-Bolale	53.33	Woldeyohannes (2008)
Jibat	49.80	Tamerat (1994)
Dindin	49.00	Simon and Girma (2004)
Bonga	45.20	Abayneh *et al*. (2003)
Menagesha	36.10	Tamerat (1994)
Jimma	33.30	Fufa (2008)
Chillimo	30.10	Tamerat (1994)

* Current studied forest

The basal area was strongly related to elevation effects in the regression model though the response of species to elevation was variable between species. Some species were negatively related, some positively related while others had a humped pattern relationship with elevation. The basal distribution of *Juniperus procera* (F = 39; $p < 0.000$) had a quadratic relationship with elevation that exhibited a unimodal pattern attaining a peak at mid elevation (about 2900 m) (Figure 23a). Peak basal area at mid elevation may be due to the dominance of *Juniperus procera* at this elevation site coupled with less harvesting of large tree at the mid elevation. The basal area of *Podocarpus falcatus* (F = 56; $p < 0.000$) was negatively and significantly related with elevation. *Podocarpus falcatus* was more distributed as a big canopy tree in the lower elevation than the middle and higher elevation sites. The distribution pattern of *Podocarpus falcatus* was limited by environmental factors might be by climatic factors thereby existed as under stroy and non-big tree form in the middle elevation. The basal area of *Juniperus procera* and *Podocarpus falcatus* was declined after 3000 m of

elevation. This might be due to climatic factors that limited the distribution range of *Juniperus procera* and *Podocarps falcatus* species along elevation gradient (Gaston, 1996). The distribution of *Erica arborea* and *Hagenia abyssinica* was positively and significantly related with elevation ($F = 69$; $p < 0.000$; $F = 70$; $p < 0.008$, respectively). Elevational variation which was the surrogate of climate might be the main factor that determined the distribution of these species at upper elevation.

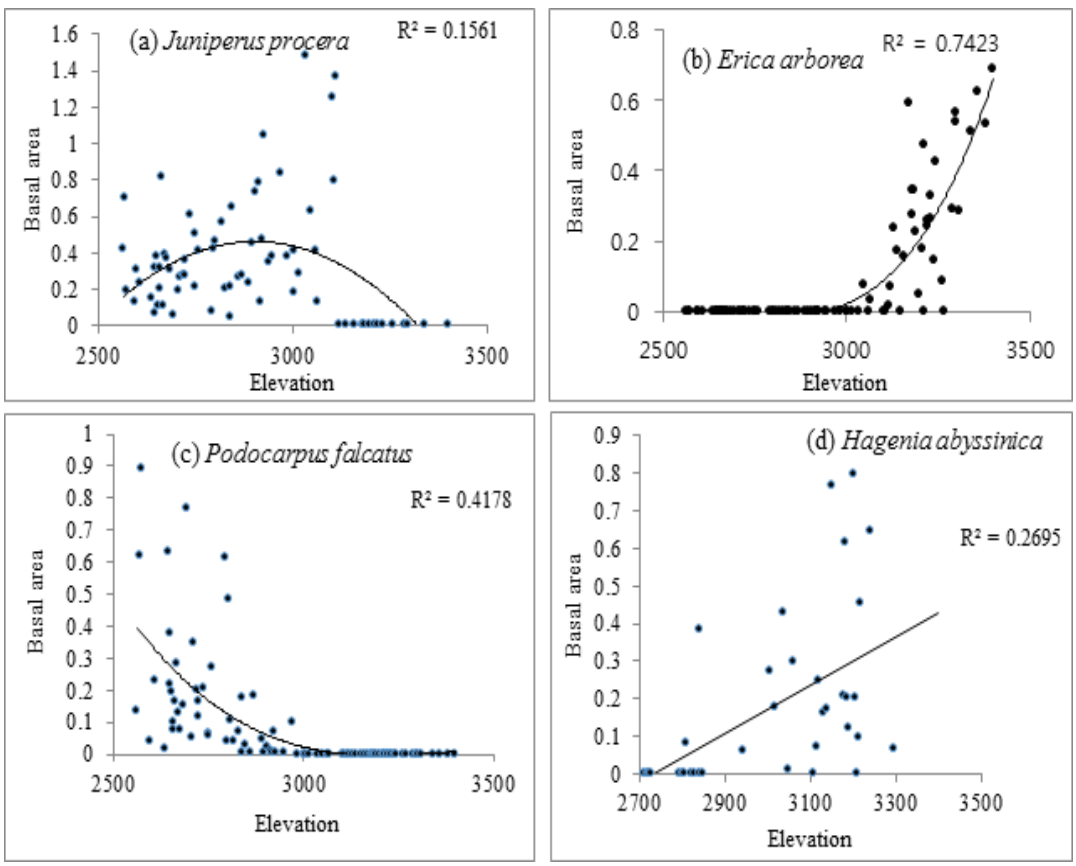


Figure 23. Basal area (BA, m^2 ha^{-1}) of four dominant trees species along elevation gradient in Adaba-Dodola forest: (a) *Juniperus procera* (b) *Erica arborea* (c) *Podocarpus falcatus* (d) *Hagenia abyssinica*

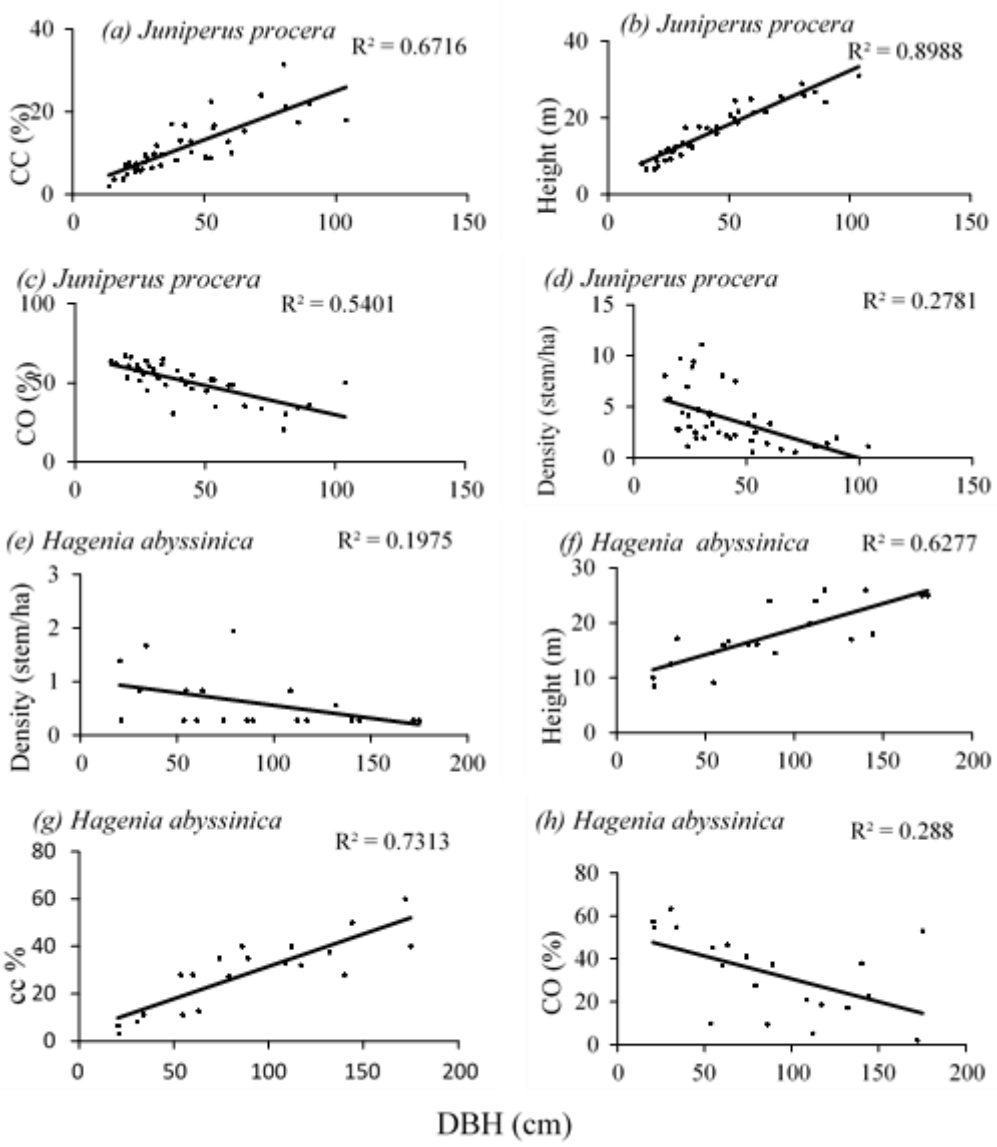
4.7.4. Relationships between tree diameter and canopy cover and canopy openness

The linear model fitted between tree diameter and canopy cover showed a strong and positive relationship. Tree diameter explained 67 %, 73 %, 34 % and 74 % of the variations observed in the canopy covers in *Juniperus procera, Hagenia abyssinica, Erica abyssinica* and *Podocarpus falcatus,* respectively (Figure 24a, g, k & o). The models were statistically significant ($p < 0.05$) for the four species. However, the diameter and the canopy openness had strong and negative relationship. The tree diameter at breast height (DBH) explained 54 %, 29 %, 30 % and 61% of the variation observed in the canopy openness in *Juniperus procera, Hagenia abyssinica, Erica abyssinica* and *Podocarpus falcatsu* trees, respectively (Figure 24c, h & n).

4.7.5. Relationship between tree diameter and height

The relationship between tree height and diameter is fundamental in determining community and ecosystem structure as well as estimates of biomass and carbon storage (Catherine *et al.,* 2015). Tree diameter and height of the investigated four woody species had strongly and positively related except for *Erica arborea*. Tree diameter explained 90 %, 63%, 11 % and 60 % of the variation of height in *Juniperus procera, Hagenia abyssinica, Erica arborea* and *Podocarpus falcatus,* respectively (Figure 24b, f, j & m). The models established were statistically significant ($p < 0.05$) in four species. The relationship between tree diameters and heights is one of the most important elements of forest structure. Information on size-class distributions of the trees within a forest stand is important for estimating product yields. The size-class distribution influences the growth potential and hence the current and future economic value of a forest (Knoebel and Burkhart, 1991). Height measurements in the field are

considerably more time consuming than DBH measurements. For this reason, generalized height-DBH relations are being developed, which permit height estimates for given tree diameters under varying forest conditions (Kramer and Akça, 1995). Height and stem diameter are components of tree size that are fundamental to processes ranging from individual performance to whole-ecosystem function. Tree diameter had positive linear relationship with canopy cover but canopy openness and tree density were negatively related to tree diameter at breast height.


(a) Juniperus procera
R² = 0.6716
CC (%)
(b) Juniperus procera
R² = 0.8988
Height (m)
(c) Juniperus procera
R² = 0.5401
CO (%)
(d) Juniperus procera
R² = 0.2781
Density (stem/ha)
(e) Hagenia abyssinica
R² = 0.1975
Density (stem/ha)
(f) Hagenia abyssinica
R² = 0.6277
Height (m)
(g) Hagenia abyssinica
R² = 0.7313
cc %
(h) Hagenia abyssinica
R² = 0.288
CO (%)
DBH (cm)

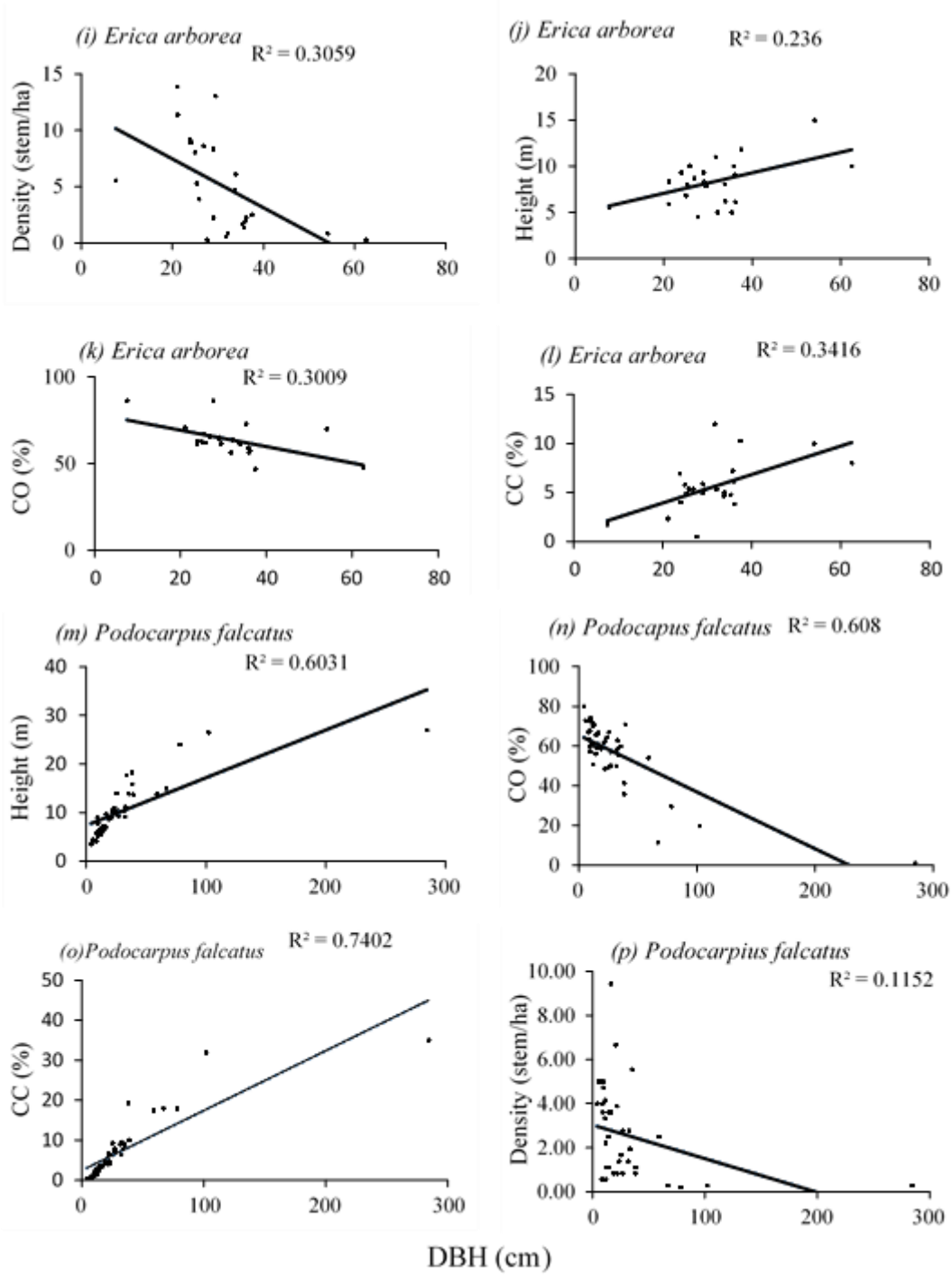


Figure 24. Relationship between tree diameters and canopy cover (a, g, o), canopy openness (c, h, k, n), height (b, f, j, m) and density (d, e, i, p).

4.7.6. Importance value index (IVI)

Importance value index was developed from the combinations of three parameters. These were relative frequency, relative density, and relative dominance (Kent and Coker, 1992). In forest structure assessment, the importance value index (IVI) is the most important parameter that helps understand forest community structural organization in relation to the competitive ability (Uniyal *et al*., 2010). It provides a more realistic result of dominance from a structural stand point (Derero *et al*., 2003). The species with the highest IVI is considered as dominant species while the species attained the second highest IVI is defined as co-dominant species (Shirsath *et al*. 2008). According to Lamprecht (1989), stands that yield the same IVI indicate the existence of the same or at least similar stand composition and structure, ecological requirements and comparable dynamics among species.

For the sake of setting priority for conservation, all woody species encountered in the forest were grouped into five IVI classes based on their total IVI values according to the criteria developed by Institute of Biodiversity Conservation and Research (IBCR) and German Technical Cooperation Agency (GTZ) for forest genetic resource conservation (FGRC) in Ethiopia (Table 15). Those species which receive lower IVI values were supposed to need high conservation priority while those species which receive high IVI values need monitoring and management (IBCR, 2002). This means that species under IVI class 5, 4 and 3 were considered for conservation priority while those under the first and second IVI classes need monitoring management. However, this does not mean that IVI values alone suffice for evaluating the conservation status of a given species. Therefore, it deserves critical revision to select as a comprehensive and standardized criterion to prioritize species for conservation in addition to this method.

Based on the IVI analysis, *Juniperus procera* and *Podocarpus falcatus* were the two top dominant tree species in forest community I (Table 16). These two forest species contributed about 37 % and 28 % of the total importance values of the community, respectively. These species were not only abundant but also frequent in their distribution in this forest community. As compared to the less abundant and less frequent species, these species accord less priority for conservation according to this criterion. In forest community I, all shrub species were found to receive low importance values (< 10 %), except *Maytenus undata*, and thus all shrub species require high priority for conservation.

In forest community II, *J. procera* and *H. abyssinica* were the two dominant tree species (Table 17). They together contributed for more than 50 % (42 % and 10 %, respectively) of the total importance values of the forest community. These two tree species were abundant and dominant and thus need less priority for conservation whereby they rather accord appropriate monitoring and management intervention. All shrub species, except *Osyris quadripartite* and *Noxia congesta*, had received lower importance values (< 10 %) and thus require high priority for conservation in this forest community. IVI is useful to compare the ecological significance of species in which high IVI value indicates high sociological structure of species in the community (Lamprecht, 1989). As a result, ecologists consider IVI as the most reasonable aspect in the vegetation study (Curtis and McIntosh, 1951). Moreover, Simon and Girma (2004) mentioned that species with the greatest importance value are the most dominant of particular vegetation.

In forest community III, about 80 % of the total importance values were contributed by four species, namely: *Juniperus procera* (25%), *Myrsine melanophloeos* (23 %), *Hypericum revolutum* (19 %) and *Hagenia abyssinica* (13 %)

species. All shrub species had received lower importance values (< 10 %) and thus require high priority for conservation in this forest community. The ecologically leading dominant species might also be the most successful species in regeneration and survival of external challenges (i.e., pathogen resistance, competition, browsing resistance, and other environmental conditions).

In the forest community IV, *Erica arborea* species had exclusively dominated the community contributing 51 % of the total importance values of the community. The four species, namely: *Erica arborea* (51%), *Hypericum revolutum* (19 %), *Hagenia abyssinica* (12 %) and *Myrsine melanophloeos* (9 %) contributed more than 90% of the total importance values of this community.

Generally, the Adaba-Dodola forest was exclusively dominated by few species. Seed supply processes such as fecundity of parent trees and widespread dispersal mechanisms might be the reason for some species to be dominant and ecologically important (Uriarte *et al*., 2005). These phenomena effected as a consequence of attractive fruits to various predators, which helped for seed dispersal and explosion of pods in the forest community (Uriarte *et al*., 2005). In all forest communities, shrubs had low IVI and thus need high priority for conservation. This indicated that there was selective cutting of shrubs.

Based on the current study, 3 (11 %), 21 (75 %) and 2 (7 %) woody plant species, respectively, were categorized as priority class 1, 2 and 3 in forest community I (i.e., they require an immediate priority for conservation) whereas, only 2 (7 %) species (i.e., *Junipersus procera* and *Podocarpus falcatus)* were categorized as priority class 5 which require no immediate conservation/restoration priority rather they require monitoring and management intervention. Based on their importance value indices, 17 (68 %) and 6 (24 %) species were categorized as the 2nd and 3rd priority

class in forest community II (which need immediate conservation), whereas only 2 (8 %) species categorized as priority class 4 and 5 (require management and monitoring intervention) (Table 17). Similarly, majority of the species required conservation intervention in community III. 10 of the 14 (71 %) species require immediate conservation priorities whereas 4 species (29 %) require monitoring and management interventions. Likewise, 9 of 13 (70 %) species require immediate conservation or restoration intervention in forest community IV whereas 4 (30 %) species require management and monitoring interventions.

In forest community I, 11 %, 75 % and 7 % of species were found under priority class 1, 2 and 3, respectively while only 7 % of the total species fallen under priority class 5. Hence, 93 % of the species in community I need immediate conservation priority. 92 %, 71 % and 70 % of the species require immediate conservation in community II, III and IV, respectively in Adaba-Dodola Afromontane forest. Overall, about 81% of the Adaba-Dodola Afromontane forest require high priority for conservation while only about 19% species were in good condition that require management intervention based on their importance value index (IVI) (Table 21 and Figure 25).

Table 15. [a]Criteria for setting IVI class and conservation priority based on IVI values

IVI value	IVI class	Priority class	Intervention required
>30	1	5	Monitoring and management
20.1-30	2	4	Monitoring and management
10.1-20	3	3	Conservation /restoration
1-10	4	2	Conservation /restoration
<1	5	1	Conservation/restoration

[a]IBCR - GTZ – Forest Genetic Resources Conservation Project (IBCR, 2002)

Table 16. Relative density (RD %), relative frequency (RF %), relative basal area (RBA %) and importance value index (IVI %) of individual species in *Podocarpus falcatus-Olea europea* forest community (C I)

Species	LF	RBA	RD	RF	IVI	IVI class	Priority
Juniperus procera	T	52.95	40.11	16.92	109.97	1	5
Podocarphus falcatus	T	34.58	31.49	16.92	82.99	1	5
Olea europaea	T	2.64	3.83	7.96	14.43	3	3
Maytenus undata	S	2.41	3.3	7.46	13.17	3	3
Ekebergia capensis	T	1.71	1.49	4.98	8.17	4	2
Osyris quadripartite	S	0.16	1.17	4.98	6.31	4	2
Myrsine melanophloeos	T	0.20	2.45	3.48	6.13	4	2
Nuxia congesta	T	0.39	1.81	2.99	5.18	4	2
Scolopia theifolia	S	0.28	1.91	2.99	5.18	4	2
Vernonia rueppellii.	S	0.18	1.81	2.99	4.97	4	2
Allophyllus abyssinicus	T	0.27	1.06	2.99	4.31	4	2
Olinia rochetiana	S	0.41	1.38	2.49	4.28	4	2
Prunus africana	T	2.09	0.43	1.49	4.01	4	2
Buddleja polystachya	T	0.18	1.06	2.49	3.73	4	2
Carissa spinarum	S	0.03	0.96	2.49	3.47	4	2
Rosa abyssinica	S	0.04	0.85	2.49	3.38	4	2
Rhamnus staddo	S	0.41	0.74	1.99	3.14	4	2
Rhus glutjnosa	T	0.09	0.53	1.99	2.61	4	2
Dovyalis abyssinica	T	0.04	1.06	1.49	2.6	4	2
Maytenus arbutifolia	T	0.09	0.53	1.49	2.12	4	2
Bersama abyssinica	T	0.02	0.32	1.49	1.83	4	2
Galiniera saxifraga	T	0.09	0.43	1	1.51	4	2
Schefflera volkensii	T	0.23	0.21	1	1.44	4	2
Myrsine Africana	S	0.01	0.43	1	1.43	4	2
Rubus steudneri	L	0	0.32	1	1.32	4	2
Hagenia abyssinica	T	0.3	0.11	0.5	0.91	5	1
Pyschotria orophila	T	0.17	0.11	0.5	0.77	5	1
Sideroxylon oxyacantbum	S	0.04	0.11	0.5	0.64	5	1
		100	100	100	300		

LF= life form

Table 17. Relative density (RD %), relative frequency (RF %), relative basal area (RBA %) and importance value index (IVI %) of individual species in *Juniperus procera-Galiniera saxifraga* forest community *(C II)*

Species	LF	RBA	RD	RF	IVI	IVI class	Priority
Juniperus procera	T	69.21	42.49	14.77	126.47	1	5
Hagenia abyssinica	T	15.48	5.20	7.95	28.64	2	4
Myrsine melanophloeos	T	2.42	7.51	7.95	17.89	3	3
Podocarphus falcatus	T	3.18	6.07	5.68	14.93	3	3
Galiniera saxifraga	T	0.93	6.94	5.68	13.54	3	3
Osyris quadripartite	S	0.36	5.49	6.82	12.67	3	3
Olea europaea	T	1.15	5.49	4.55	11.19	3	3
Nuxia congesta	S	0.55	4.05	5.68	10.27	3	3
Maytenus undata	S	1.31	1.45	4.55	7.30	4	2
Ekebergia capensis	T	0.18	2.31	4.55	7.03	4	2
Schefflera volkensii	T	1.01	1.45	4.55	7.00	4	2
Erica arborea	T/S	2.98	1.16	2.27	6.41	4	2
Myrsine africana	S	0.65	2.31	3.41	6.37	4	2
Inula confertiflora	S	0.02	1.73	3.41	5.17	4	2
Hypericum revolutum	T	0.11	1.16	3.41	4.68	4	2
Dombeya torrida	T	0.19	1.45	2.27	3.91	4	2
Olinia rochetiana	S	0.10	0.87	2.27	3.24	4	2
Dovyalis abyssinica	T	0.01	0.58	2.27	2.86	4	2
Buddleja polystachya	S	0.05	0.58	1.14	1.77	4	2
Lobelia rhychnchopetalum	T	0.07	0.29	1.14	1.49	4	2
Myrica salicifolia	T	0.04	0.29	1.14	1.47	4	2
Schefflera myriantha	T	0.03	0.29	1.14	1.45	4	2
Prunus africana	T	0.01	0.29	1.14	1.43	4	2
Rhus glutjnosa	T	0.00	0.29	1.14	1.43	4	2
Rubus steudneri	L	0.00	0.29	1.14	1.43	4	2
		100	100	100	300		

Table 18. Relative density (RD %), relative frequency (RF %), relative basal area (RBA%) and importance value index (IVI %) of individual species in Myrsine melanophloeos- Hagenia abyssinica forest community (C III)

Species	Lf	RBA	RD	RF	IVI	IVI class	Priority
Juniperus procera	T	45.66	18.30	11.11	75.07	1	5
Myrsine melanophloeos	T	8.09	37.91	22.22	68.22	1	5
Hypericum revolutum	T	12.37	27.45	16.67	56.49	1	5
Hagenia abyssinica	T	27.64	3.92	8.33	39.90	1	5
Schefflera volkensii	T	3.20	2.61	8.33	14.15	3	3
Erica arborea	T/S	1.99	1.96	5.56	9.51	4	2
Podocarphus falcatus	T	0.01	1.31	5.56	6.88	4	2
Galiniera saxifraga	T	0.12	1.31	2.78	4.20	4	2
Vernonia rueppellii	S	0.10	1.31	2.78	4.19	4	2
Maytenus undata	S	0.60	0.65	2.78	4.03	4	2
Nuxia congesta	T	0.15	0.65	2.78	3.58	4	2
Osyris quadripartite	S	0.01	0.65	2.78	3.44	4	2
Inula confertiflora	S	0.01	0.65	2.78	3.44	4	2
Maesa lanceolata	T/S	0.00	0.65	2.78	3.43	4	2
Rubus steudneri	S	0.00	0.65	2.78	3.43	4	2
		100	100	100	300		

Table 19 Relative density (RD %), relative frequency (RF %), relative basal area (RBA %) and importance value index (IVI %) of individual species in Erica arborea- Hypercum revolutum forest community *(C IV)*

Species	Lf	RBA	RD	RF	IVI	IVI class	Priority
Erica arborea	T/S	58	66.5	27.3	151.8	1	5
Hypericum revolutum	T	14.8	18.4	23.4	56.54	1	5
Hagenia abyssinica	T	19.6	2.93	14.3	36.8	1	5
Myrsine melanophloeos	T	3.02	6.94	15.6	25.55	2	4
Schefflera volkensii	T	3.53	1.7	7.79	13.02	3	3
Gnidia glauca	S	0.05	0.62	2.6	3.26	4	2
Inula confertiflora	S	0.02	1.08	1.3	2.4	4	2
Juniperus procera	T	0.76	0.31	1.3	2.37	4	2
Nuxia congesta	S	0.09	0.62	1.3	2.01	4	2
Discopodium pennlnervium	S	0.02	0.31	1.3	1.62	4	2
Osyris quadripartite	S	0.01	0.31	1.3	1.62	4	2
Buddleja polystachya	S	0.1	0.15	1.3	1.55	4	2
Olinia rochetiana	S	0.01	0.15	1.3	1.47	4	2
		100	100	100	300		

Table 20. List of species under each priority class of conservation and management in respective forest community

***Podocarpus falcatus-Olea europea* forest community (C I)**				
Priority for conservation				
1	2	3	4	5
Hagenia abyssinica *Pyschotria orophila* *Sideroxylon oxyacantbum*	*Ekebergia capensis* *Osyris quadripartite* *Myrsine melanophloeos* *Nuxia congesta* *Scolopia theifolia* *Vernonia rueppellii.* *Allophyllus abyssinicus* *Olinia rochetiana* *Prunus africana* *Buddleja polystachya* *Carissa spinarum* *Rosa abyssinica* *Rhamnus staddo* *Rhus glutjnosa* *Dovyalis abyssinica* *Maytenus arbutifolia* *Bersama abyssinica* *Galiniera saxifraga* *Schefflera volkensii* *Myrsine Africana* *Rubus steudneri*	*Olea europaea* *Maytenus undata*		*Juniperus procera* *Podocarphus falcatus*
***Juniperus procera-Galiniera saxifraga* forest community (C II)**				
1	2	3	4	5
	Maytenus undata *Ekebergia capensis* *Schefflera volkensii* *Erica arborea* *Myrsine africana* *Inula confertiflora* *Hypericum revolutum* *Dombeya torrida* *Olinia rochetiana* *Dovyalis abyssinica* *Buddleja polystachya*	*Myrsine melanophloeos* *Podocarpus falcatus* *Galiniera saxifraga* *Osyris quadripartite* *Olea europaea* *Nuxia congesta*	*Hagenia abyssinica*	*Juniperus procera*

	Lobelia rhychnchopetalum *Myrica salicifolia* *Schefflera myriantha* *Prunus africana* *Rhus glutjnosa* *Rubus steudneri*			
***Myrsine melanophloeos-Hagenia abyssinica* forest community (C III)**				
1	2	3	4	5
	Podocarphus falcatus *Galiniera saxifraga* *Vernonia rueppellii* *Maytenus undata* *Nuxia congesta* *Osyris quadripartite* *Inula confertiflora* *Maesa lanceolata* *Rubus steudneri*	*Schefflera volkensii*		*Juniperus procera* *Myrsine melanophloeos* *Hypericum revolutum* *Hagenia abyssinica*
***Erica arborea-Hypercum* revolutum forest community (C IV)**				
1	2	3	4	5
	Gnidia glauca *Inula confertiflora* *Juniperus procera* *Nuxia congesta* *Discopodium pennlnervium* *Osyris quadripartite* *Buddleja polystachya* *Olinia rochetiana*	*Schefflera volkensii*	*Myrsine melanophloeos*	*Erica arborea* *Hypericum revolutum* *Hagenia abyssinica*

Table 21. Number (N) and percentage (%) of species categorized under each priority class for conservation based on IVI.

Priority class	Community I		Community II		Community III		Community IV		Overall (%)
	N	%	N	%	N	%	N	%	
1	3	11	0	0	0	0	0	0	2.75
2	21	75	17	68	9	64	8	62	67.25
3	2	7	6	24	1	7	1	8	11.50
4	0	0	1	4	0	0	1	8	3.00
5	2	7	1	4	4	29	3	23	15.75
Total	28	100	25	100	14	100	13	100	100

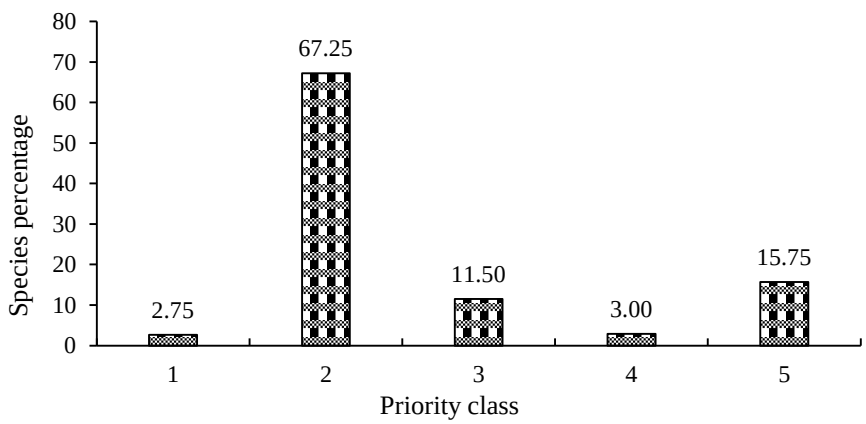


Figure 25. Mean percentage of species under each priority class for conservation based on IVI

4.7.7. Vertical stratification

Forests can be stratified vertically into vegetation layers of different heights and species occupying different canopy levels at maturity (Whittaker, 1975) (Figure 27-30). Thus, it is possible to distinguish different tree species such as emergent, upper canopy, lower canopy and understory trees and shrub layers. The vertical stratification

of trees in this study was examined based on the IUFRO classification scheme (Lembandgut, 1958; cited in Lamprecht, 1989). The top height was used for determining the vertical structure of trees and hence, the tree heights were stratified into three different layers: upper, middle and lower based on the longest tree in respective forest community. Accordingly, upper layer trees comprised of individual tree/shrub species that attain a height greater than 2/3 of the top height of a given forest. The middle layer/ strata was formed by individual tree/shrub species with a height < 2/3 and > 1/3 of the top height in a given forest. The lower layer was composed of individual tree/shrub species with a height less than 1/3 of the top height tree.

Accordingly, the top height tree in forest community I was *Podocarpus falcatus* with 45-meter height. Thus, trees in the lower, middle and upper layers in community I were those in the height array of < 15 m, 15-30 m and > 30 m, respectively. In community II, *Juniperus procera* was the top tree with the maximum height of 31 m. Hence, trees in the lower, middle and upper layers were those in the height array of < 10 m, 10−21 m and > 21 m, respectively. Similarly, the top height tree in forest community III was *Juniperus procera* with 27.2-meter height. Thus, trees in the lower, middle and upper layers in community III were those in the height array of < 9 m, 9-18 m and > 18 m, respectively. In community IV, *Juniperus procera* was the top tree with the maximum height of 27 m. Hence, trees in the lower, middle and upper layers were those in the height array of < 9 m, 9-18 m and > 18 m, respectively.

The vertical distribution of species density varied among forest communities. The largest density was contributed by the lower layer species. About 78 % of the total density in community I was contributed by the the lower storey (Table 22). The most two dominant wood species in the lower layer (< 15 cm) of community I were *Juniperus procera* (68 stems /ha, 34 %) and *Podocarpus falcatus* (64 stems/ha, 32 %).

The middle layers also dominated by *Juniperus procera* (36 stems /ha, 63 %) and *Podocarpus falcatus* (18 stems / ha, 31 %) species. 22 % of the total density was contributed by the middle layer species in community I whereas the proportion of density contributed by the upper layer to total density was negligble. Similarly, the upper layer of community I consisted of only two species: *Podocarpus falcatus* (0.6 stems /ha, 67 %) and *Juniperus procera* (0.3 stems /ha, 33 %). The lower layer of community II was dominated by *Juniperus procera* (31 stems/ha, 21%) and *Myrsine melanophloeos* (7 stems/ha, 10%*). Juniperus procera* (6 stems/ha, 51%) had dominated the middle layer of community II followed by *Hagenia abyssinica* (2.5 stems /ha, 21 %). At the upper layer of the community, still *Juniperus procera w*as found to be highly dominant (13 stems/ha, 89 %) followed by *Hagenia abyssinica* tree species.

At the lower layer of community III, 61% (14 stems/ha) of the total density of the population was contributed by *Myrsine melanophloeos* whereas 20 % (5 stems /ha) of the total density was from *Hypercum revolutum.* Majority of the middle layer of community III forest were occupied by *Hypercum revolutum* (7 stems/ha, 58 %) followed by *Myrsine melanophloeos* (2 stems /ha, 13 %). Majority of the upper layer of this community was occupied by *Juniperus procera (*5 stems /ha, 81 %).

In all communities, the highest density was found in the lower storey followed by the middle storey. The upper storey had relatively the lowest density in all communities except in community II. Similarly, more number of species was found in the lower and the middle storeys whereas the upper storey was occupied by fewer species. Kelbessa and Soromessa (2008) observed similar result in Bonga Afromontane forest of Ethiopia. This phenomenon indicated that numerous species were unable to reach the

upper layer may be due to changing environmental conditions and / or anthropogenic disturbances.

There was no regular distribution of species in the three layers in the community I. For instance, only 2 species (*Juniperus procera* and *Podocarpus falcatus)* were distributed in all storeys. These two species are described as species with regular distribution (Lamprecht, 1972, cited in Lamprecht, 1989). Five species (18 %) were distributed only in lower and middle storeys. About 21 of 28 (75 %) of the species in forest community I were confined to the lower storey only (Appendix Table 1). In general, the lower layer contributed about 52-78 % of the total density in forest communities whereas middle and upper layers, respectively contributed 13-38% and 0-20 % (Table 22). This might be due to the high selective exploitation of the middle layered trees for fencing and house construction and the upper layer large trees for timber production by the local people.

Table 22. Density (D, individual ha-1), number (N) and percentage of species in the vertical layers of forest communities in Adaba-Dodola Afromontane forest

Forest layers	Community I				Community II				Community III				Community IV			
	D	%	N	%	D	%	N	%	D	%	N	%	D	%	N	%
Upper	1	0	2	5	15	16	4	11	6	20	2	10	1.4	1	3	15
Middle	58	22	8	22	12	13	7	19	13	28	6	29	69	38	5	25
Lower	203	78	27	73	69	72	25	69	24	52	13	62	110	61	12	60
Total	261	100	37	100	96	100	36	100	43	100	21	100	180	10	20	100

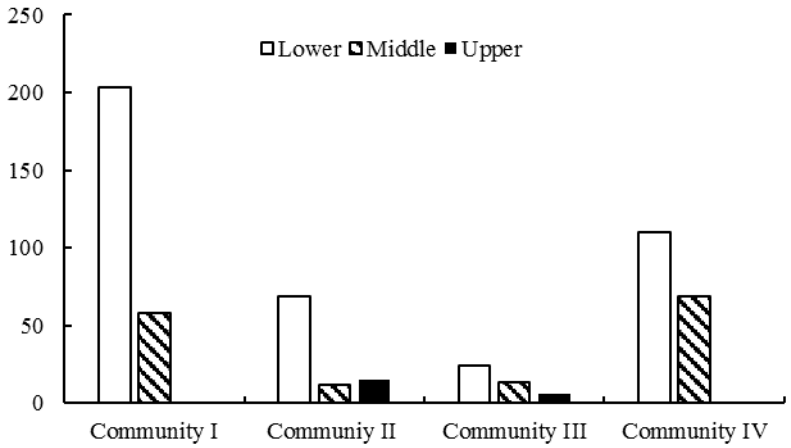


Figure 26. Proportion of density (stem/ha) of species by three forest layers (lower, middle and upper)

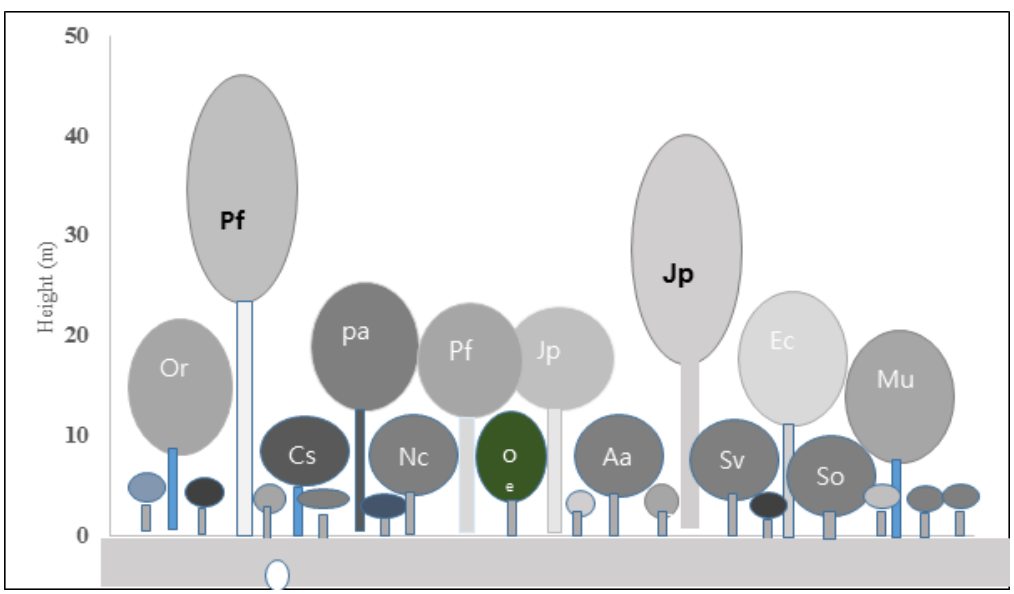


Figure 27. Profile diagram of vertical layers of *Podocarpus falcatus-Olea europea* forest community at 2565-2915m.

Pf=*Podocarphus falcatus;* Jp= *Juniperus procera;* Or= *Olinia rochetiana;* Pa= *Prunus Africana;* Ec= *Ekebergia capensis;* Mu= *Maytenus undata;* Cs= *Carissa spinarum;* Nc= *Nuxia congesta;* Aa= *Allophyllus abyssinicus;* Sv= *Schefflera volkensii;* So= *Sideroxylon oxyacantbum*

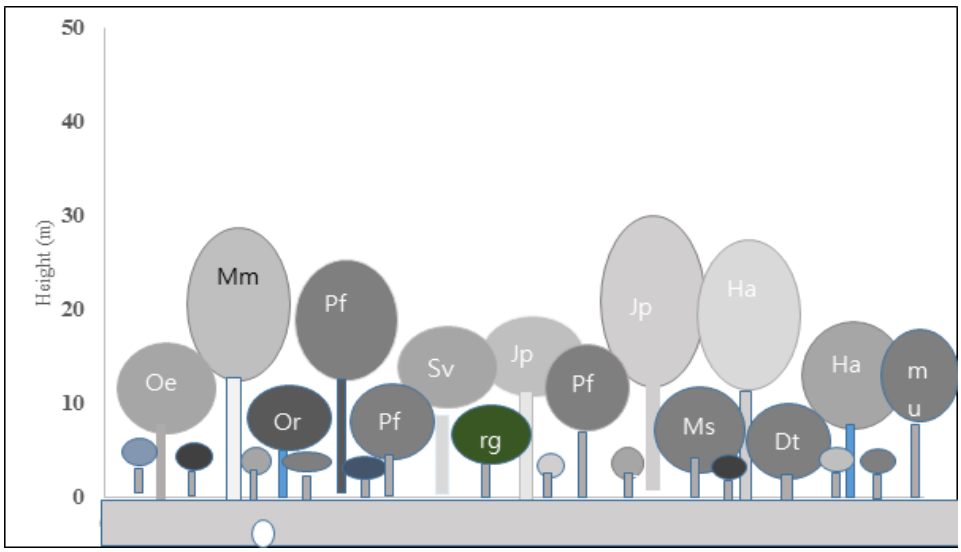


Figure 28. Profile diagram of vertical layers of *Juniperus procera- Galiniera saxifrage* forest community at 2825-3115m.

Pf=*Podocarphus falcatus;* Jp= *Juniperus procera;* Or= *Olinia rochetiana;* Mu= *Maytenus undata;* Sv= *Schefflera volkensii;* Mm= *Myrsine melanophloeos;* Oe= *Olea europaea;* rg= *Rhus glutjnosa;* Ms= *Myrica salicifolia;* Dt= *Dombeya torrida;* Ha= *Hagenia abyssinica;* etc

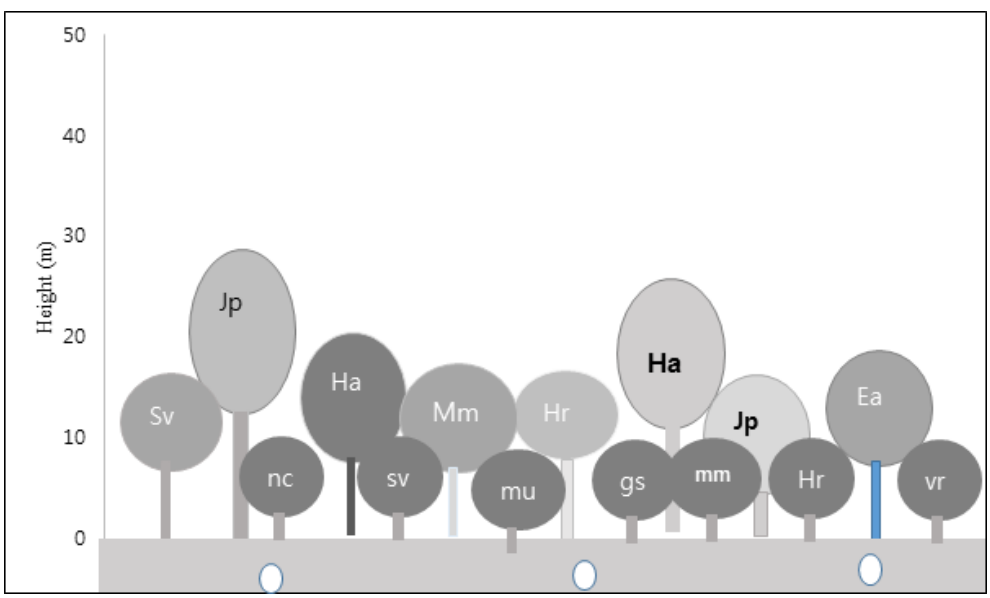


Figure 29. Profile diagram of vertical layers of *Myrsine melanophloeos- Hagenia abyssinica* forest community at 2925-3275m.

Jp= *Juniperus procera;* Mu= *Maytenus undata;* Sv= *Schefflera volkensii;* Mm= *Myrsine melanophloeos;* Ha= *Hagenia abyssinica;* nc= *Nuxia congesta;* SV= *Schefflera volkensii;* Hr= *Hypericum revolutum;* gs= *Galiniera saxifrage;* Vr= *Vernonia rueppellii,* Ea= *Erica arborea; etc*.

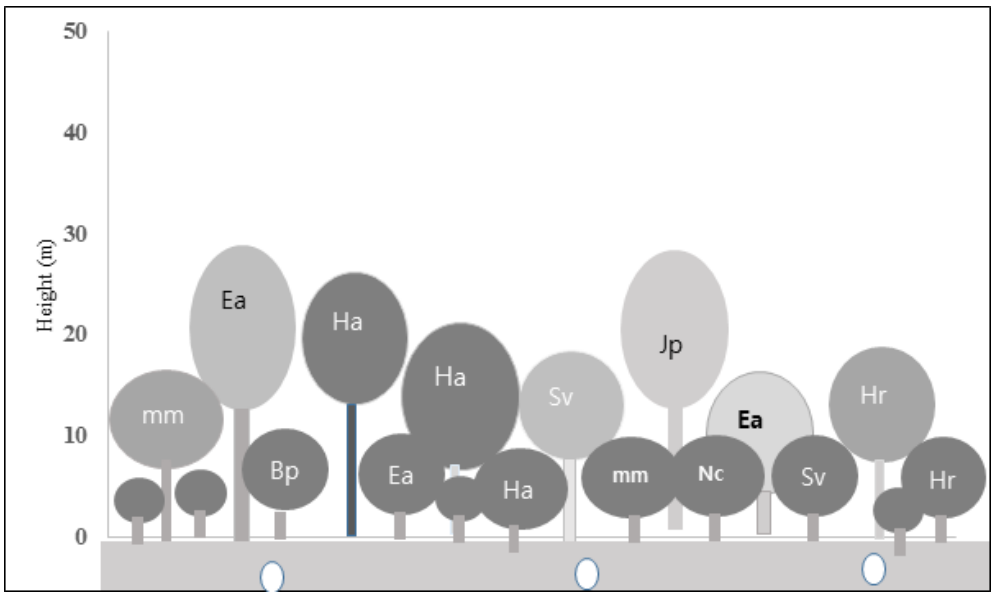


Figure 30. Profile diagram of vertical layers of *Erica arborea- Hypercum revolutum* forest community at 3065-3400 m.

Jp= *Juniperus procera;* Sv= *Schefflera volkensii;* Mm= *Myrsine melanophloeos;* Ha= *Hagenia abyssinica;* Nc= *Nuxia congesta;* Hr= *Hypericum revolutum;* Ea= *Erica arborea;* Bp= *Buddleja polystachya; etc.*

4.7.8. Woody plant population structure analysis

Population structure refers to the distribution of individual species in an arbitrarily diameter-height size classes to provide the overall regeneration profile of species (Peters, 1996). According to Tamrat (1993), structural patterns of population could be interpreted as an indication of variation in population dynamics that may happen due to inherent characters or due to humans and livestock interventions. The structural patterns of population have significant implications to their management, sustainable use and conservation (Simon and Girma, 2004).

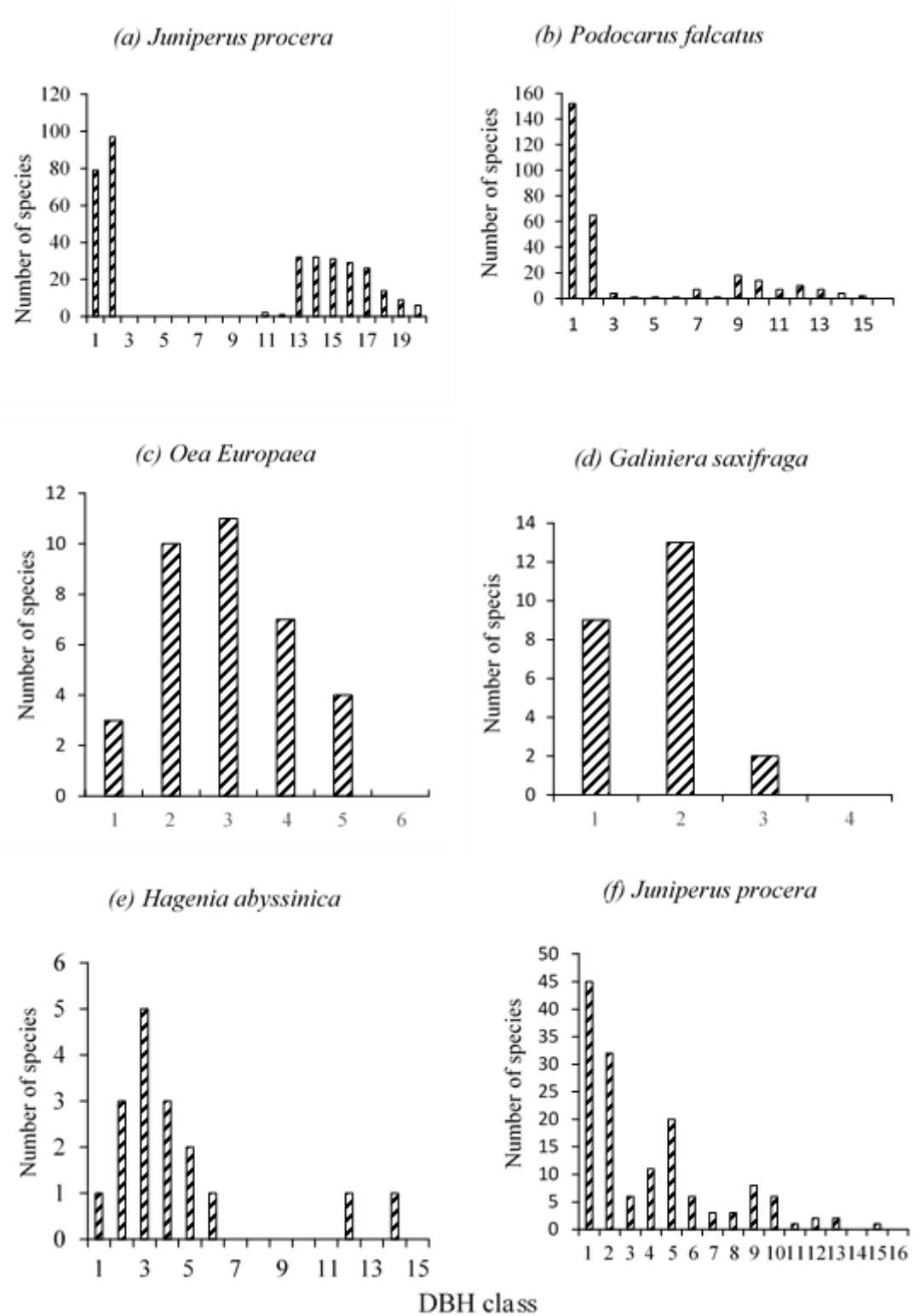
In the current study, the patterns of population structure were illustrated by the three most dominant indicator species selected from each clustered community based on their indicator values (IV). The analysis of population structure of all tree

species in Adaba-Dodola forest was shown in five structural patterns (Figure 31). The first pattern was reversed J-shape, which indicated more number of species at the lower diameter (DBH) classes and decreased gradually towards the higher DBH classes. This pattern indicates continuous reproduction and recruitment (Feyera *et al*., 2007). The second pattern was the interrupted reversed J-shape which showed good regeneration but at interrupting pattern. In this pattern, more number of the species at the lower DBH class was observed with declining at the highest DBH class but the increment was interrupted. The third pattern was bell-shape, which showed more number of individuals in the middle diameter classes and less number of individuals towards the lower and higher ends of the diameter classes. The fourth pattern was interrupted Bell-shape where the number of species was higher at the mid diameter but in the interrupted manner. The fifth pattern was irregular-shape, which showed a combination of different patterns and characterized with the absence (missing) of plants in some diameter classes irregularly.

The reversed J-shape pattern was represented by *Myrsine melanophloeos* species (Figure 31 i & l) both in forest community III and community IV. In this pattern, number of woody species was generally declined with increasing diameter classes implying good recruitment of species. The interrupted reversed J-shape pattern was represented with *Podocarpus falcatus* (Figure 31b) in the forest community I. In this pattern, there was more number of species at lower DBH class whereas the middle DBH class species were negligible and then the number of species increased slightly and declined at the larger DBH class. This pattern indicated selective harvesting of medium and big sized trees for *pole* and for timber production.

Juniperus procera (Figure 31a & g) exhibited an irregular representation of individuals in DBH classes both in community I and III. In community I, it was

characterized with the complete absence (missing) of the species at the middle DBH classes whereas it was generally irregularly missing at all DBH classes in community III. This pattern indicated discontinuous recruitment. *Olea europaea* in community I (Figure 31c), *Galiniera saxifraga* in community II (Fig 37d), *Hypercum revolutum* in community III (Figure 31h), *Erica arborea* and *Hypercum revolutum* in community IV (Figure 31 J & k) exhibited a bell-shape pattern of distribution. In this pattern, lower DBH classes had low density followed by a progressive increase in the number of individuals towards the medium classes, and then a progressive decrease towards the higher DBH classes. According to Feyera *et al*. (2007), a bell shape distribution pattern indicates discontinuous distribution of species which may be due to with the removal of trees of preferred size.


(a) Juniperus procera
Number of species
120
100
80
60
40
20
0
1 3 5 7 9 11 13 15 17 19
(b) Podocarus falcatus
Number of species
160
140
120
100
80
60
40
20
0
1 3 5 7 9 11 13 15
(c) Oea Europaea
Number of species
12
10
8
6
4
2
0
1 2 3 4 5 6
(d) Galiniera saxifraga
Number of specis
14
12
10
8
6
4
2
0
1 2 3 4
(e) Hagenia abyssinica
Number of species
6
5
4
3
2
1
0
1 3 5 7 9 11 13 15
(f) Juniperus procera
Number of species
50
45
40
35
30
25
20
15
10
5
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
DBH class

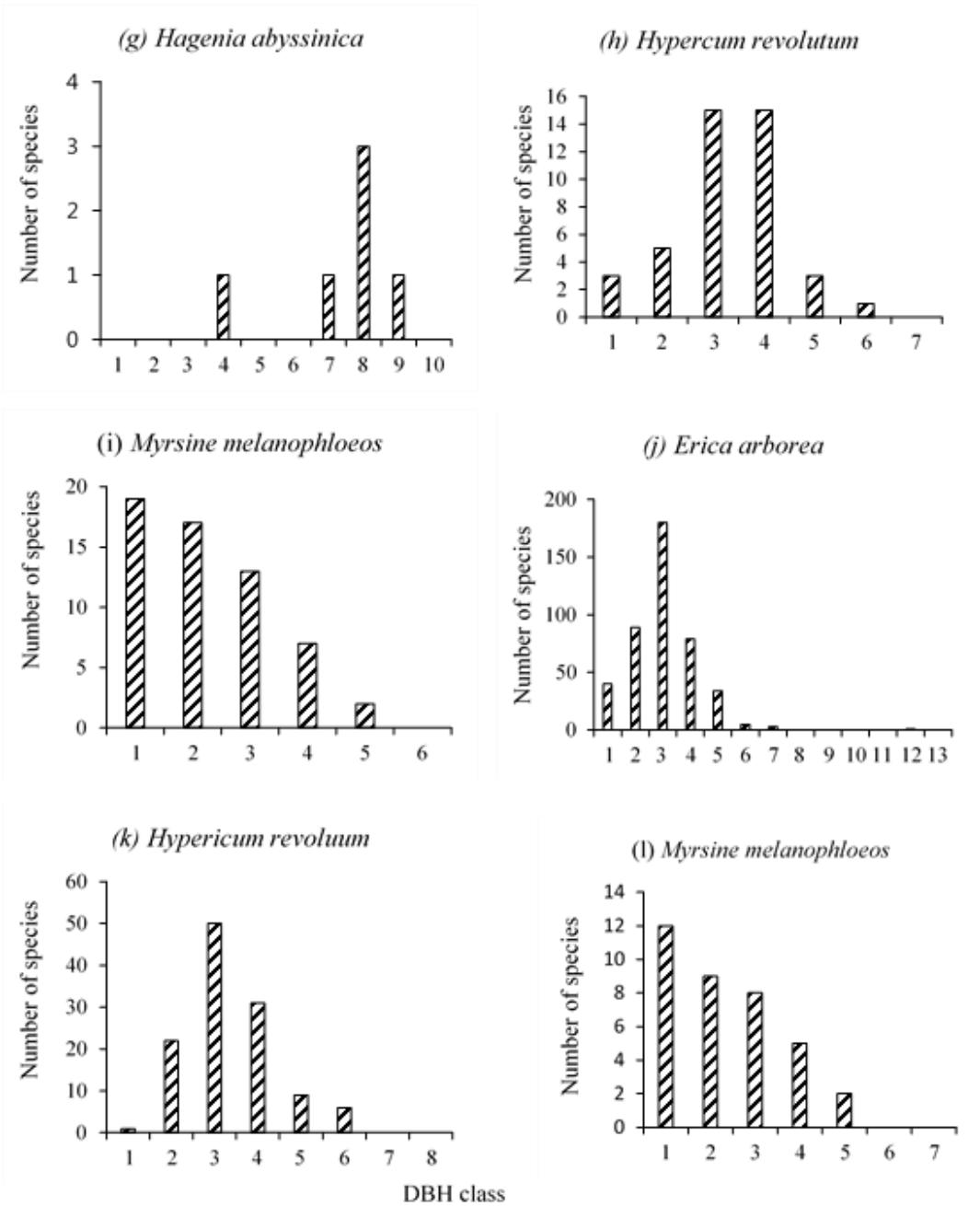


Figure 31. Representative patterns of population structure and representative tree species in C1 (a-c) CII (c-e) CIII (f-h) and C IV (i-l) of Adaba-Dodola forest

1= 2- 10 cm, 2 = 10.1-20 cm, 3 = 20.1-30 cm, 4 = 30.1-40 cm, 5 = 40.1-50 cm, 6 = 50.1-60 cm, 7 = 60.1-70 cm, 8 =70.1-80, 9= 80.1-90, 10= 90.1-100, etc. C = community

4.7.9. Forest regeneration

Composition, distribution and density of seedlings, saplings and adult trees in the forest indicate the status of regeneration of the forest (Table 24). The sustainability of natural forests depends on the regeneration capacity of each age group in the forest. The regeneration or recruitment condition of woody species is one of the major factors that are useful to assess forest conservation status (Taye *et al.*, 2003).

The regeneration status of individual tree species in four forest communities of the Adaba-Dodola forest was presented in Table 23 and Figure 32. A total of 645 seedlings (17,917 individual ha^{-1}) and 217 saplings (964.44 individual ha^{-1}) were recorded in all plots of the study area. The overall seedling density ranged between a maximum of 9750 individual ha^{-1} in community I and a minimum of 250 individual ha^{-1} in community III, whereas sapling density varied between a maximum of 457.78 individual ha^{-1} in community I and a minimum of 31.11 individual ha^{-1} in community IV. Regeneration status of tree species in terms of proportions of seedlings, saplings and adults varied among different communities. In forest community I, density of seedling (individual ha^{-1}) was high (9750 individual ha^{-1}), followed by saplings (457.78 individual ha^{-1}) and adult trees and shrubs (261.11 individual ha^{-1}). In community I, majority (52 %) of the species showed no regeneration at all, 24.14 % fair regeneration, 20 % good regeneration and 3.45% poor regeneration status. The lack and/or poor regeneration status of most species in this community might be due to the high anthropogenic disturbance (grazing/browsing and cutting) activities in the site.

Forest community II had a seedling density of 4388.89 individual ha^{-1}, sampling density of 435.56 individual ha^{-1} and an adult tree density of 96.11 individual ha^{-1}. Majority of the species of the community showed no regeneration followed by

good regeneration potential. 44.44 % of the total species were categorized as no regenerating, 37.04 % as good, 7.41 % as fair, 7.41 % as poor and 3.7 % as new regeneration status. The regeneration potential in community II was better than community I. 12 of 27 (44 %) species in this community were not regenertaing at all. These include *Buddleja polystachya, Dombeya torrida, Erica arborea, Hagenia abyssinica, Hypericum revolutum, Lobelia rhychnchopetalum, Myrica salicifolia, Nuxia congesta, Olinia rochetiana, Prunus africana, Rubus steudneri* and *Schefflera volkensii*. Four species showed poor and fair regeneration (i.e., *Galiniera saxifraga* and *Olea europaea* as fair regeneration and *Osyris quadripartite* and *Rhamnus staddo* as poor regeneration). 10 of 27 (37%) species had good regeneration potential in this forest community.

In the forest community III, the seedling density was 250 individual ha^{-1} and the sapling density was 40 individual ha^{-1}. Similar to community I and II, community III had more number of species with no regeneration status (66.67 %), whereas only a single species had good regeneration status. A total of 26.66 % species had poor and fair regeneration status. In forest community IV, 50 % of the total population had fair regeneration, 35.71 % no regeneration, 7.14 % poor regeneration and 7.14% good regeneration status. In general, about 41.27% of the total species were not regenerating at all, 25.40 % species had fair regeneration status and 9.52% had poor regeneration status in Adaba-Dodola Afromontane forest. Less than a quarter (22.22 %) of the total species was in good regeneration status. Generally, more than 75 % of the population of Adaba-Dodola forest had no good regeneration status based on the proportions of seedlings, saplings and adults. Compared to other forest communities, community II had more number of species having in good regeneration condition whereas community III and IV had very few species having good regeneration condition.

Table 23. Floristic composition and plant regeneration status based on proportions of plant growth stages

Floristic composition and plant regeneration status based on proportions of plant growth stages. S_D = seedling density, Sa_D = sapling density, T_D = adult tree/shrub density. We followed Shankar (2001) and Chauhan *et al*. (2008) to determine regeneration status within categories of tree life form stages: (i)good regeneration - if number of seedlings > saplings > adult tree/shrubs; (ii) fair regeneration - if number of seedlings > or < saplings < adult tree/shrubs; (iii) poor regeneration - if the species occupy only at sapling life forms and if no seedlings (number of saplings may be >, < or = number of adults; (iv) no regeneration - if individuals of species are present only in adult form and (v) new regeneration or not abundant– if individual of species has only seedlings or saplings but no adults. In this present study, adults referred to matured trees or shrubs.

Species	S_D	Sa_D	T_D	Regeneration status
Community I				
Allophyllus abyssinicus (Hochst.) Radlk.	0.00	0.00	2.78	No regeneration
Bersama abyssinica Fressen.	833.33	31.11	0.83	Good regeneration
Buddleja polystachya Fressen.	0.00	0.00	2.78	No regeneration
Carissa spinarum L.	0.00	0.00	2.50	No regeneration
Dovyalis abyssinica (A. Rich.) Warb	388.89	8.89	2.78	Good regeneration
Ekebergia capensis Sparm.	194.44	0.00	3.89	Fair regeneration
Galiniera saxifraga	0.00	0.00	1.11	No regeneration
Hagenia abyssinica (Bruce) J. Gmel.	0.00	0.00	0.28	No regeneration
Inula confertiflora A. Rich.	0.00	8.89	0.00	Poor regeneration
Juniperus procera L.	416.67	53.33	104.72	Fair regeneration
Maytenus arbutifolia (Hochst. ex A Rich.)	1388.89	0.00	1.39	Fair regeneration
Maytenus undata (Thunb.) Blakelock	1111.11	4.44	8.61	Fair regeneration
Myrsine Africana L.	1472.22	97.78	1.11	Good regeneration
Myrsine melanophloeos (L.) R. Br.	444.44	62.22	6.39	Good regeneration
Nuxia congesta R. Br. ex fresen.	0.00	0.00	4.72	No regeneration
Olea europaea subsp. Cuspidate	805.56	0.00	10.00	Fair regeneration
Olinia rochetiana A. Juss.	0.00	0.00	3.61	No regeneration
Osyris quadripartite Decn.	0.00	0.00	3.06	No regeneration
Podocarphus falcatus (Thunb.)	2388.89	164.44	82.22	Good regeneration
Prunus africana (Hook. f.)	0.00	0.00	1.11	No regeneration
Pyschotria orophila	0.00	0.00	0.28	No regeneration
Rhamnus staddo A. Rich.	55.56	0.00	1.94	Fair regeneration
Rhus glutjnosa A. Rich.	27.78	0.00	1.39	Fair regeneration
Rosa abyssinica Lindley	0.00	0.00	2.22	No regeneration
Rubus steudneri Schweinf	0.00	0.00	0.83	No regeneration
Schefflera volkensii (Harms. ex.Engl.)	0.00	0.00	0.56	No regeneration
Scolopia theifolia Gilg.	222.22	26.67	5.00	Good regeneration
Sideroxylon oxyacantbum Baill.	0.00	0.00	0.28	No regeneration
Vernonia rueppellii Sch. Bip.	0.00	0.00	4.72	No regeneration
Sub-total density	9750.00	457.78	261.11	
Community II				
Buddleja polystachya Fressen.	0.00	0.00	0.56	No regeneration

Dombeya torrida (J.F. Gmel)	0.00	0.00	1.39	No regeneration
Dovyalis abyssinica (A. Rich.)	27.78	17.78	0.56	Good regeneration
Ekebergia capensis Sparm.	27.78	4.44	2.22	Good regeneration
Erica arborea L.	0.00	0.00	1.11	No regeneration
Galiniera saxifraga	444.44	0.00	6.67	Fair regeneration
Hagenia abyssinica (Bruce) J. Gmel.	0.00	0.00	5.00	No regeneration
Hypericum revolutum Vahl	0.00	0.00	1.11	No regeneration
Inula confertiflora A. Rich.	27.78	44.44	1.67	Good regeneration
Juniperus procera L.	111.11	44.44	40.83	Good regeneration
Lobelia rhychnchopetalum	0.00	0.00	0.28	No regeneration
Maytenus undata (Thunb.) Blakelock	222.22	4.44	1.39	Good regeneration
Myrica salicifolia A.Rich.	0.00	0.00	0.28	No regeneration
Myrsine Africana L.	2055.56	195.56	2.22	Good regeneration
Myrsine melanophloeos (L.) R. Br.	1000.00	88.89	7.22	Good regeneration
Nuxia congesta R. Br. ex fresen.	0.00	0.00	3.89	No regeneration
Olea europaea subsp. Cuspidate	277.78	0.00	5.28	Fair regeneration
Olinia rochetiana A. Juss.	0.00	0.00	0.83	No regeneration
Osyris quadripartite Decn.	0.00	4.44	5.28	Poor regeneration
Podocarphus falcatus (Thunb.)	55.56	13.33	5.83	Good regeneration
Prunus africana (Hook. f.)	0.00	0.00	0.28	No regeneration
Rhamnus prinoides L'Herit	27.78	0.00	0.00	New regeneration
Rhamnus staddo A. Rich.	0.00	4.44	0.00	Poor regeneration
Rhus glutjnosa A. Rich.	55.56	8.89	0.28	Good regeneration
Rubus steudneri Schweinf	0.00	0.00	0.28	No regeneration
Schefflera myriantha (Bak.) Drake	55.56	4.44	0.28	Good regeneration
Schefflera volkensii (Harms. ex.Engl.)	0.00	0.00	1.39	No regeneration
Sub-total density	4388.89	435.56	96.11	
Community III				
Erica arborea L.	0.00	0.00	0.83	No regeneration
Galiniera saxifraga	0.00	0.00	0.56	No regeneration
Hagenia abyssinica (Bruce)	0.00	0.00	1.67	No regeneration
Hypericum revolutum Vahl	83.33	0.00	11.67	Fair regeneration
Inula confertiflora A. Rich.	0.00	0.00	0.28	No regeneration
Juniperus procera L.	0.00	17.78	7.78	Poor regeneration
Maesa lanceolata Forssk	27.78	0.00	0.28	Fair regeneration
Maytenus undata (Thunb.)	0.00	0.00	0.28	No regeneration
Myrsine melanophloeos (L.)	138.89	17.78	16.11	Good regeneration
Nuxia congesta R. Br. ex fresen.	0.00	0.00	0.28	No regeneration
Osyris quadripartite Decn.	0.00	0.00	0.28	No regeneration
Podocarphus falcatus (Thunb.) Mirb	0.00	4.44	0.56	Poor regeneration
Rubus steudneri Schweinf	0.00	0.00	0.28	No regeneration
Schefflera volkensii (Harms. ex.Engl.)	0.00	0.00	1.11	No regeneration
Vernonia rueppellii Sch. Bip. ex Walp.	0.00	0.00	0.56	No regeneration
Sub-total density	250.00	40.00	42.50	

Community IV				
Buddleja polystachya Fressen.	0.00	0.00	0.28	No regeneration
Discopodium pennlnervium	0.00	0.00	0.56	No regeneration
Erica arborea L.	27.78	8.89	119.72	Fair regeneration
Gnidia glauca (Fresen.)	83.33	0.00	1.11	Fair regeneration
Hagenia abyssinica (Bruce)	27.78	0.00	5.28	Fair regeneration
Hypericum revolutum Vahl	2555.56	0.00	33.06	Fair regeneration
Inula confertiflora A. Rich.	305.56	0.00	1.94	Fair regeneration
Juniperus procera L.	222.22	0.00	0.56	Fair regeneration
Myrsine Africana L.	0.00	4.44	0.00	Poor regeneration
Myrsine melanophloeos (L.)	250.00	17.78	12.50	Good regeneration
Nuxia congesta R. Br. ex fresen.	0.00	0.00	1.11	No regeneration
Olinia rochetiana A. Juss.	0.00	0.00	0.28	No regeneration
Osyris quadripartite Decn.	0.00	0.00	0.56	No regeneration
Schefflera volkensii (Harms. ex.Engl.)	55.56	0.00	3.06	Fair regeneration
Sub-total density	3527.78	31.11	180.00	
Total density (ha)	17916.67	964.44	579.72	

Table 24. Species regeneration status and percentage in each forest community in Adaba-Dodola forest

Forest community	Good regeneration	Fair regeneration	Poor regeneration	New regeneration	No regeneration
I	20.69	24.14	3.45	0.00	51.72
II	37.04	7.41	7.41	3.70	44.44
III	6.67	13.33	13.33	0.00	66.67
IV	7.14	50.00	7.14	0.00	35.71

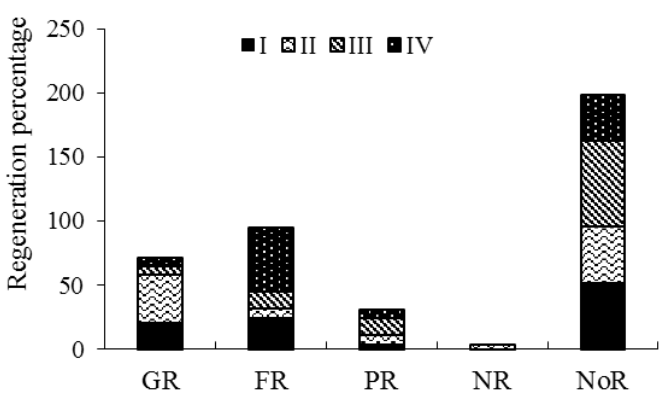


Figure 32. Regeneration of status of species in each community

GR= good regeneration; FR= fair regeneration; PR= poor regeneration; NR= new regeneration; NoR = no regeneration

4.8. Soil seed bank floristic composition and diversity

Investigation of soil seedbank species composition, abundance and floristic similarity between seed banks and standing vegetation are important indicators for potential of natural regeneration from the soil seed banks (Welling *et al*., 1988). In the present study, 39 germinant species with 22 families were observed from soil seed banks (Table 25). Of these germinant species, 18 (46 %) were woody species (7 trees, 10 shrubs and 1 tree/ shrub), 7 (18%) graminoids, 12 (31%) herbs and 2 (5%) sedges. The largest family recorded from the soil seed bank was Poaceae (7 species) followed by Fabaceae (5 species), Myrsinaceae, Rosaceae and Lamiaceae (3 species each). Herbs comprised the largest group (30.77 %) of the total emergent species. Shrubs were the next largest group among species emerged from the seed bank comprising 25.64 % of the total species emerged. Trees, sedges and trees /shrubs comprised 17.95 %, 5.13 % and 2.56 % of the total richness of the emergent in that order.

In terms of individual abundance of emerged species, herbs comprised the largest (36.74 %) life forms and followed by graminoids (36.61 %), sedges (19.41 %), trees (4.03 %), shrubs (3.08 %) and tree/shrubs (0.13 %) (Table 25). The most frequent life forms in the seed bank were herbs (96 %), graminoids (84 %) and sedges (71 %), while the frequency of shrubs, trees and trees /shrubs were 38 %, 34 % and 3.3 %, respectively (Table 25). The low germination rate of woody species in the study site might be because of the fact that seeds of many montane rainforest tree and shrub species have short-duration viability and are quickly exhausted from the soil seed bank during prolonged land use (Holl *et al*., 2000). Furthermore, most seeds are typically produced within fleshy fruits (Figure 33) (e.g. *Juniperus procera, Podocarpus falcatus, Ekebergia capensis,* in the present study*)* so that their seed dispersal is mediated by frugivorous vertebrates that do not frequently visit open vegetation (Da Silva *et al*.,

1996). In some instances, seeds might be infected or eaten by insects or birds or seeds may have hard coat cover that might also attribute to the less germination rate. For instance, Aerts (2008) noted that seeds of *podocarpus falcatus* collected from the ground are often infected with the fungus *Penicillium claviforme*, which reduces the germination rate. These scenarios might be the case for the poor germination rate of *Podocarpus falcatus* tree which was one of the most dominant trees in middle and lower elevation sites of the present study area. Degafi and Berhanu (2014) tested the viability of *Podcarpus falcatus* seed collected from the soil bank and found that the viability of *Podocarpus falcatus* was very poor (2.11%). Abdella (2004) mentioned the main reason for poor viability in *Podocarpus falcatus* seed was the death of the seed by seed borne fungal diseases in the soil seed bank.

Figure 33. Seed of Podocarpus falcatus tree; fleshy

Table 25. Total individuals, number of species and frequency of species emerged from seed bank

Growth form	Total ind. emerged	% of species emerged	No. of spp. emerged	% of ind	Emerged Frequency
Graminoids	845	36.61	7	17.95	76(84)
Herbs	848	36.74	12	30.77	84(96)
Sedges	448	19.41	2	5.13	64 (71)
Shrubs	71	3.08	10	25.64	34(38)
Trees	93	4.03	7	17.95	31(34)
Trees / shrubs	3	0.13	1	2.56	3(3.3)
Total	2308	100	39	100	

Values in the parenthesis are the frequency percentages of each life form in the sampling plots whereas values outside the parenthesis are the frequency of occurrence of each life form (number of plots in which each life form observed

4.8.1. Soil seed bank flora density and abundance

The mean soil seedling density in the four vegetation clusters ranged from 645 to 2104 seedlings / m^2. The mean density of graminoids ranged from 93 to 1075 seedlings/m^2, herbs from 187 to 647 seedlings / m^2, sedges from 125 to 353 seedlings / m^2. The density of shrubs and trees ranged from 1.67 to 58 and 21 to 95 seedlings/m^2, respectively. There was a significant difference of mean seedling density among clustered vegetation communities ($p < 0.05$) (Table 26). Significantly, the largest mean tree seedling density (95 seedlings / m^2) was recorded from *Juniperus procera-Galiniera saxifraga* community (community II) which was located at the middle elevation. This might be mainly attributed to the less anthropogenic disturbance in this community. Because the ANOVA analysis and the RDA model indicate that the impact of disturbance in this community was less and did not significantly explain the variation. The lowest mean density (21 seedlings / m^2) of tree seedling was recorded

in *Podocarpus falcatus-Olea europea* community (commnity I) followed by *Erica arborea- Hypercum revolutum* community (community IV) (33 seedlings / m^2).

Significant ($p < 0.05$) and the largest mean density of grasses (1075 seedlings / m2), herbs (642 seedlings / m^2) and sedges (353 seedlings / m^2) species were recorded in *Erica arborea-Hypercum revolutum,* that is, in the upper elevation zone. The largest mean overall density of emergent seedlings was recorded for herbaceous and grasses lifeforms. Whereas the least over all mean density records were from trees, shrubs and tree/shrub species. From grasses and herbs species, Trifolium burchellianum (17, 267 seedlings / m^2) had the highest total seedling density followed by *Cynodon dactylon* (11,333 seedlings / m^2), *Eragrostis paposa* (10,400 seedlings / m^2), *Cyperus pauper* (8,167 seedlings / m^2), *Geranium arabicum* (7,100 seedlings / m^2) and *Phaenantheocium koestlinii* (4,900 seedlings /m^2).

It was observed that the germinant of annual weed and herb species were dominant in the soil seed bank of higher and lower elevation zones. These species are hardy pioneer plants that need very little nutrients to survive, grow rapidly and fill the damaged area. They can readily acclimate to bare soil, and respond vigorously even on the poorest environmental conditions (Elgar *et al*., 2014). The less woody species density but high density of annual weedy species in the seed bank in the high and low elevational sites might be due to the climatic and disturbance influences experienced in these areas that might have created a favourable condition for grasses and herbs to suppress the regeneration of trees and shrubs. However, in the middle elevation zone, in the *Juniperus procera-Galiniera saxifraga* community, where there was relatively low human disturbance impact and intermediate climatic conditions, the density of these pioneer species was low as compared to other communities. However, density of woody species was high in *Juniperus procera-Galiniera saxifraga* community and

elevation zone than in the other community. In agreement with this study, Bertiller *et al*. (1995) noted that woody species are relatively abundant in less disturbed areas. Demel and Granström (1996) also reported more density of grasses and sedges (cyperus and grass species) at that the upper elevation zones.

Seed banks in many tropical forests are dominated by pioneer species, particularly most of the seed bank species in the Afromontane forests are herbs (Demil and Granström, 1996). In the current study, more than 90 % of the individual proportion of germinated seedling from the seedbank was annual grasses and herbaceous species (herbs and sedges) (Table 26). In agreement with the current result, Demil and Granström (1996) also reported that majority (around 60 %) of the species in the seed bank were annuals. Degafi and Birhanu (2014) investigated less number of woody species in seedbank in the northeastern Ethiopian Afromontane forest. Demel (2005) mentioned one of the reasons for less wood species might be due to relatively short residence time of woody species in the soil.

The woody species with mean seedling density below 100 seedlings / m^2 in the seed banks of the current study include *Podocarpus falcatus* (66.67 seedlings / m^2), *Prunus africana* (33.33 seedlings / m^2*), Rosa abyssinica* (33.33 seedlings / m^2), *Solanum incanum* (66. 67 seedlings / m^2) and *Datura stramonium (*33.33 seedlings /m^2*).* The top five tree species with the highest soil seedling density in the soil seed bank include *Juniperus procera* (1133.33 seedlings / m^2), *Hypericum revolutum* (800 seedlings / m^2), *Hagenia abyssinica* (433.33 seedlings / m^2), *Myrsine melanophloeos* (333.33 seedlings / m^2) and *Dombeya torida* (300 seedlings / m^2). Shrub species with highets emergent seeedlings in the soil soil seed bank include *Vernonia rueppellii (*567 seeldings / m^2) *Solanum marginatum (*467 seeldings / m^2) *Inula confertiflora (*433

seeldings / m^2), *Achyranthes aspera (*300 seeldings / m^2) and *Myrsine africana (*267 seeldings / m^2) (Table 27).

Table 26. ANOVA for density (Mean ± SE) of emergent seedlings in soil seedbank of Adaba-Dodola Afromontane forest

Life forms	Forest community				
	I	II	III	IV	Overall mean
Grasses	143.21± 77.72^{b}	93.33±127.72^{b}	233.34±142.79^{b}	1075.00±90.31^{a}	386.22±56.40
Herbs	340.74±71.57^{b}	186.67±117.60^{c}	545.83±131.48^{ab}	641.67±83.16^{a}	428.73±51.93
Sedges	167.90±49.00^{b}	233.33±80.52a^{b}	125.00±90.0^{b}	353.33±56.94^{a}	219.89±35.56
Shrubs	55.55±8.97^{a}	36.67±14.74^{a}	58.33±16.49^{a}	1.67±10.43^{b}	38.05±6.511
Trees	20.99±25.81^{b}	95.00±29.99^{a}	37.50±47.42^{ab}	33.33±42.42^{ab}	46.70±18.73
T/S	3.70±1.34^{ns}	0.00±2.20^{ns}	0.00±2.46^{ns}	00±1.56^{ns}	0.93±0.97
Total	732.10±150.58^{b}	645.33±247.43^{b}	1000±276.64^{b}	2104.67±174.96^{a}	1120.52±109.27

T/S= tree / shrub

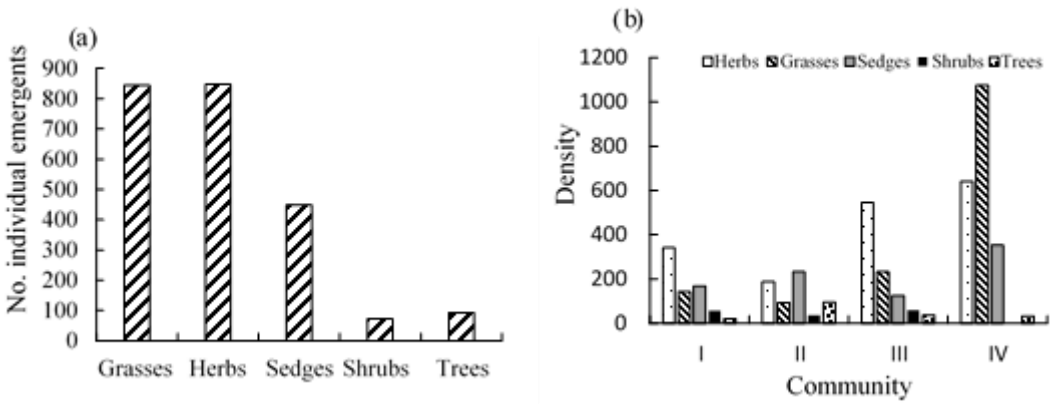


Figure 34. (a) Total individual and (b) mean density (mean/m^2) of emergent seedlings in soil seed bank

Table 27. Density (seedling / m^2) of soil seed bank emergent species per forest communities (I- IV) and soil layers (0-3, 3-6, 6-9 cm)

Species	I			II			III			IV			Total density
	0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm	0-3cm	3-6cm	6-9cm	
Achyranthes aspera	66.67	200	33										300
Ajuga integrifolia		33											33
Campanula edulis							33			33			67
Crotalaria pycnostachya				33		33						33	100
Cynodon dactylon	33.33						33			4533	3867	2867	11333
Cyperus Pauper	233.33	300.	100	400	100		33	133	333	1533	2167	2833	8167
Cyperus sesquiflorus	1500.00	1700	700	833	567	433	133		367	133	300	100	6767
Datura stramonium		33											33
Dombeya torida	100.00	100	67					33					300
Eleusine floccifolia		33											33
Eragrostis paposa	1867	700	433	167	67		400	467	100	3467	2100	633	10400
Eragrostis schweinfurthii	267	233		267	33				33			33	867
Eurphobia dumalis	33	33											67
Geranium arabicum	1433	1067	400	633	300	233	333	300	233	1067	533	567	7100
Hagenia abyssinica	67			33		33				100	200		433
Hypericum revolutum	333				133	133	200	33		100	167		800
Inula confertiflora	33	33	67	33	33		200	33					433
Juniperus procera	100									967	33	33	1133
Leucas martinicensis		33											33
Maesa lanceolata	100												100
Medicago polymorpha		33											33
Myrsine africana	100					67		100					267
Myrsine melanophloeos									33		300		333

Pennisetum clandestinum										200			200
Phaenantheocium koestlinii	33	33	33		267	133	67	133	400	833	1467	1500	4900
Plantago lanceolata	33						133		67	700	100		1033
Podocarpus falcatus	67												67
Prunus africana		33											33
Rosa abyssinica				33									33
Satureja abyssinica	167	200											367
Solanum incanum	33								33				67
Solanum marginatum	167	67	33	33	67			67	33				467
Sparmannia ricinocarpa	33	33			33								100
Sporobolu pilifenas	200						167	67					433
Trifolium burchellianum	2767	1267	1167		400	233	1233	1067	933	3067	2300	2833	17267
Trifolium quartinianum	267	33	33	67						833	333	433	2000
Trifolium schimperi		100						33			33		167
Urtica simensis	100												100
Vernonia rueppellii	300	200	67										567
Total density	10133	6500	3133	2533	2000	1300	2967	2467	2567	17567	13900	11867	76933

4.8.2. Vertical distribution of soil seed banks in soil layers

The results of ANOVA analysis showed that soil depth had a significant effect on soil seed bank density ($p < 0.05$). Soil seedling density was significantly ($p < 0.05$) declined with increasing soil depth for all life forms except for sedge species. The highest mean seedling density was recorded from the upper layer (0-3 cm) of the soil depth (527 seedlings / m^2); whereas the lower soil layer (6-9 cm) had significantly exhibited the lowest mean density of seedling (325 seedlings / m^2) (Table 28 and Figure 35). The highest mean seedling density was recorded for herb species (454 seedling / m^2) and followed by grasses (450 seedling / m^2) whereas the lowest density was recorded for trees/shrubs (1.59 seedling / m^2). In the upper layer, the seed bank density accounted for 43 % of the total mean seedling density of all layers. This observation was consistent with several previous studies in Ethiopia (Feyera and Demel, 2002; Getachew *et al*., 2004) who recorded more seedling density and composition at the upper layer. In agreement with the present study, Demil and Granström (1996) also reported the highest densities at the upper layer (0-3 cm) in Ethiopia. Tessema *et al*. (2016) also reported that the upper soil layer had more number of emerged seeds compared with the deeper soil layer.

There was variation between lifeforms in relation to the vertical distribution of emergent seedlings in the seedbank layers. For instance, seedlings of some woody species were almost entirely confined to the upper layer (e.g, *Podocarpus falcatus*, *Rosa abyssinica*, *Crotalaria pycnostachya*, *Solanum incanum* and *Maesa lanceolate).* On the otherhand, some species had seedlings which were well distributed in all soil layers (e.g. *Juniperus procera, Dombeya torida, Hagenia abyssinica, Hypericum revolutum, Achyranthes aspera, Inula confertiflora, Myrsine Africana, Solanum marginatum* and *Vernonia rueppellii).* Most herbaceous and grass species were

concentrated in the first layer of the soil depth, while sedge species was almost uniformly distributed in all layers. In the contrary to Demil and Granström (1996), not only trees and shrubs seedlings but also herbs, grasses and sedges were found at shallower layer (upper layer) in the present study area.

Table 28. Density (number / m^2, mean ± SE) of seedling emergent per soil layer (depth) in soil seedbank of Adaba-Dodola Afromontane forest

Growth Habit	Soil depth (cm)			Total
	0-3	3-6	6-9	
Grasses	198.94 ± 29.65^{a}	145.64 ± 29.19^{a}	106.321± 30.90^{b}	450.90
Herbs	205.29 ± 20.15^{a}	126.15 ± 19.84^{b}	122.99 ± 21.00^{b}	454.43
Sedge	76.19 ± 15.03^{ns}	81.03 ± 14.80^{ns}	83.91 ± 15.67^{ns}	241.13
Shrubs	16.93 ± 3.60^{a}	13.85 ± 3.54^{a}	6.90 ± 3.54^{b}	37.68
Trees	28.04 ± 9.47^{a}	15.89 ± 9.32a^{b}	5.17 ± 9.87^{b}	49.1
Tree/shrub	1.59 ± 0.57^{a}	0.00 ± 0.56^{b}	0.00 ± 0.56^{b}	1.59
Total mean	526.98 ± 48.76^{a}	382.56 ± 48.00^{b}	325.29 ± 50.82^{b}	1234.83

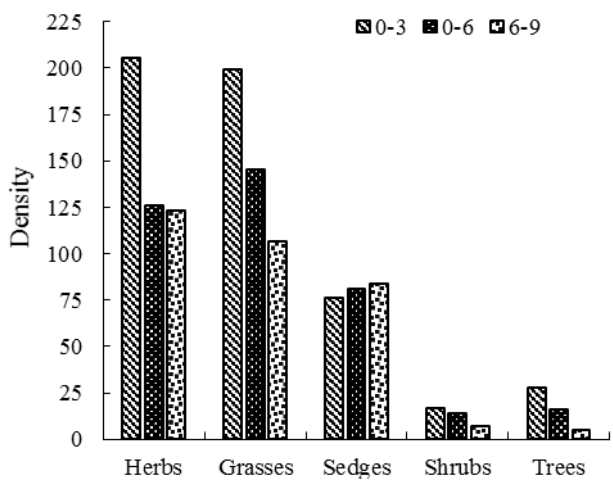


Figure 35. Mean density (number/m^2) of the vertical distribution of the emergent seedlings in the soil seed bank

4.8.3. Soil seed bank species richness and diversity

There were more species richness and diversity of grass and herbaceous species in the soil seed bank of forest community I and IV (Table 29 and Figure 36). In the contrary, these two forest communities had less richness and diversity of trees and shrubs in the soils seed bank. The middle elevation community, the forest community II, had more tree and shrub richness and diversity in the soil seed bank but less richness and diversity for grass and herbs lifeforms. This result noted that soil related factors might have limited the diversity and richness of woody species in the soil seed bank while favouring for the regeneration and survival of annual grasses and herbs. In community IV, the lowest pH value was recorded whereby the low pH creates the toxic metals (such as Al^{3+}) that can hinder nitrification (Bobbink *et al*., 2010b) which in turn results in an increased accumulation of ammonium. Many graminoids can withstand high ammonium concentrations and be able to suppress the germination or regeneration of the less ammonia resistant woody seedlings (Vandenberg *et al.,* 2008). Likewise, the high total nitrogen recorded in community IV might have also contributed for the germination of more graminoids. In several studies, high nitrogen depositions leading to soil acidification have been identified as playing a major role in increasing graminoids germination (Bobbink and Williams, 1987; Carroll *et al.,* 2003). Aerts (1990) stated that the grass encroachment and competition affects succession, changes species composition and often leads to monospecific stands and thereby reducing plant diversity.

Another possibility was that the increased herbaceous competitiveness under more nitrogen limits the growth and survival of woody seedlings (Cohn *et al*., 1989). Furthermore, Cohn *et al*. (1989) and Debain *et al*. (2005) demonstrated in competition experiments that the negative effect of high nitrogen on seedling performance is caused

by the intensification of herbaceous competition on woody seedlings. Woody cover is therefore predicted to be negatively affected by enhanced nitrogen deposition (Sankaran *et al*., 2008).

In the forest community I (the lower elevation zone forest community) where heavy anthropogenic disturbances such as grazing, cutting and human settlement were observed, more density, richness and diversity of grasses and herbs were recorded from the soil seed bank. The dominance of anthropogenically influenced sites by herbs and grasses/sedges supported an argument that they need very little nutrients to survive and able to shed their seed and grow rapidly to fill the damaged area or bury their seed in the seed bank. Belsky (1992) similarly noted that anthropogenic disturbances such as heavy grazing and tree cutting encourage grass encroachment. This ultimately results in the dominance of annual weeds and herbs in the soil seed banks (Tessema *et al*., 2016). Solomon *et al*. (2006) stated that the colonization of soil seed bank with annual weeds and herbs resulted in reducing the seed contribution of woody species to the soil seed banks. Several recent soil seed bank studies, in agreement with the present finding, shown that the seeds of woody species were rare in seed banks compared with herbaceous and grass species in various tropical forests that were heavily disturbed (Tekle and Bekele, 2000; Figueroa *et al*., 2004; Solomon *et al*., 2006, Esmailzadeh *et al*., 2011). Those invasions by large herbaceous species cause the greatest changes in other seed banks, greatly reducing the species richness and density of seed banks.

Table 29. Soil seed bank species richness and diversity statistics by growth habit in four clustered forest communities

Diversity indices for life forms	Forest community			
	I	II	III	IV
Grasses				
Richness, *S*	6	3	5	5
Shannon index, *H*	2.81	1.38	1.88	2.79
Evenness index, *E*	0.80	0.50	0.64	0.96
Herbs				
Richness *S*	11	3	5	6
Shannon index, *H*	3.05	1.83	1.88	2.70
Evenness index, *E*	0.87	0.66	0.64	0.93
Sedges				
Richness, *S*	2	2	2	2
Shannon index, *H*	2.51	1.83	1.76	2.57
Evenness index, *E*	0.71	0.66	0.60	0.87
Shrubs				
Richness, *S*	4	8	6	1
Shannon index, *H*	1.72	2.82	0.36	0
Evenness index, *E*	0.80	0.62	0.12	0
Trees				
Richness, *S*	2	6	3	3
Shannon index, *H*	0.47	1.70	0.94	0.80
Evenness index, *E*	0.13	0.59	0.32	0.29

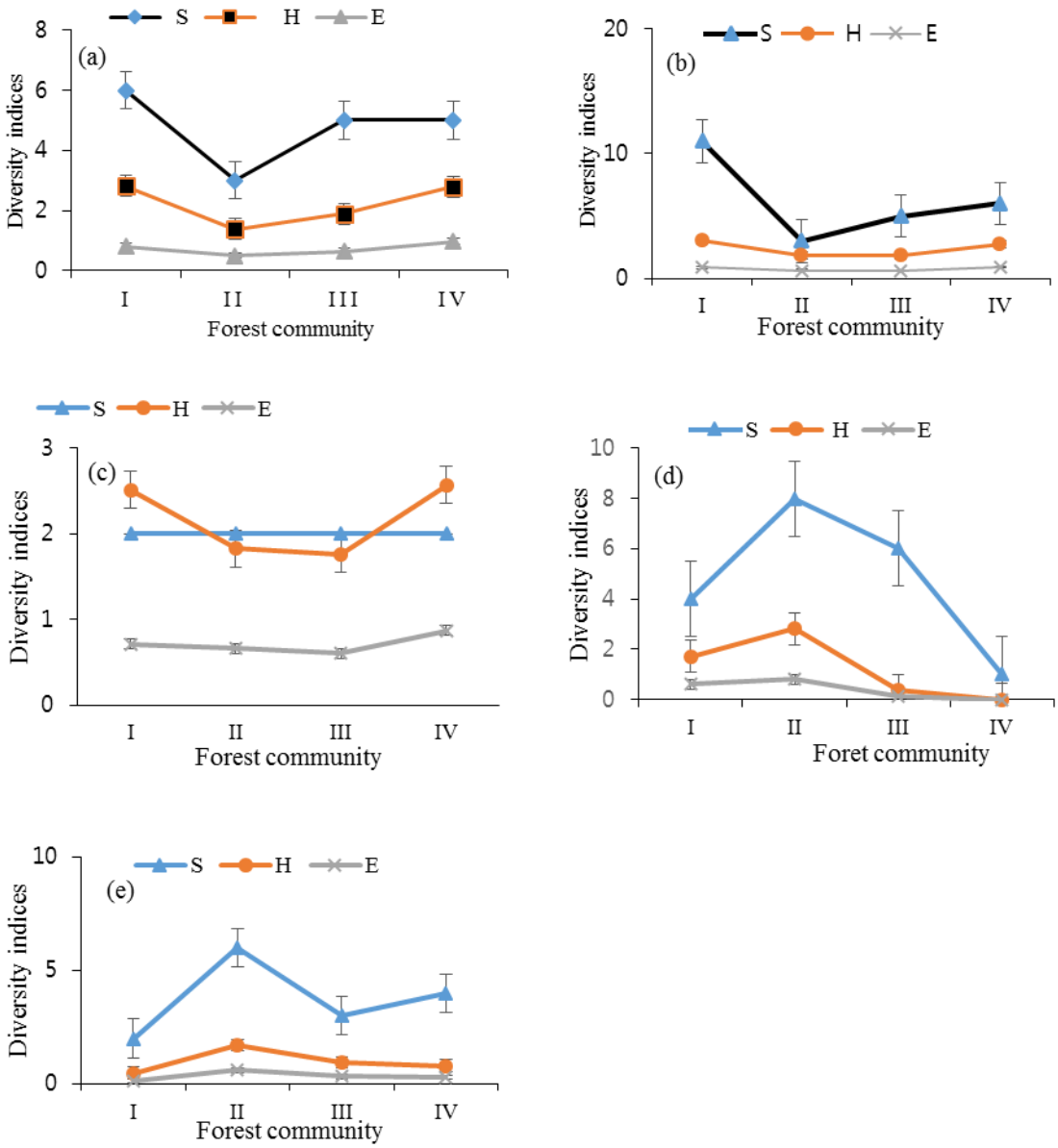


Figure 36. Species richness (S), Shannon diversity (H) and evenness (E) of seed bank life forms in four forest communities: (a) grasses (b) herbs (c) sedges (d) shrubs and (e) trees

4.8.4. Relationship of soil seed bank species with environmental and disturbance factors

Ordination analysis indicated that RDA axis 1 was positively correlated with pH (r = 0.763; $p < 0.001$), negatively correlated with total nitrogen (r = -0.652; $p < 0.001$), electrical conductivity (r = -0.586; $p < 0.01$), soil moisture (r=-0.635) and elevation (-0.812) (Table 30). Axis 2 showed positive correlation with settlement distance (r = 0.618), negative correlation with cutting (-0.569) and grazing (-0.471). The first RDA axis had large eigenvalue and coefficient of correlation, and cumulatively the explanatory variables explained 16% of variance in seed bank species composition (Table 30).

Variables with higher influence on the variability of soil seed bank appeared on graph with longer vectors. The composition of species was found to correspond with different environmental and disturbance variables at different degree of influences. In the first RDA axis, the variance of SSB species composition was mainly determined (explained) by pH, elevation, soil moisture (MC), electrical conductivity (EC) and total nitrogen (TN) (Table 30 and Figure 37). The variance of second axis was, however, mainly determined (explained) by the settlement distance, cutting and grazing. Since the pH, elevation, soil moisture, electrical conductivity and total nitrogen were strongly correlated with axis1, this axis was mainly explained by soil and topographic factors (generally named as environmental gradient), and hence the first axis was called as environment gradient (component). Likewise, settlement distance, cutting and grazing were strongly correlated with species composition along axis 2, and the variation of this axis was mainly explained by human disturbance and thus named as human disturbance gradient.

The relationship of germinated plant species and environmental and disturbance factors was drawn based on the first two ordination axes. The SSB species could reflect the preference to certain soil nature and disturbance factors showing that both factors will influence soil seed bank plants. The species with strong correlation with axis 1 (environmental gradient) include S*olanium nigrum, Solanum marginatum, Juniperus procera, Cyperus spp, Hagenia abyssinica, pennisetum clandestinum, Plantago lanceolata, Trifolium spp.*and *Cynodon dactylon*. Similarly, some species such as *Crotalaria pycnostachya, Rosa abyssinica, Vernonia rueppellii, Denbeya torida, Podocarpus falcatus, Datura stramonium, Maesa lanceolata, Medicago polymorpha, Trifolium spp, Eragrostis spp.,* etc. had strong correlation with axis 2. These species were more associated with human disturbance factors. Hence, both human disturbance factors and environmental factors were found to be important factors explaining the SSB species composition in the Afromontane forest communities of the study area.

Table 30. Pearson correlation coefficients (r) of RDA axes with environmental and disturbance factors

Variable	Axis 1	Axis 2	Axis 3
Eigenvalue	3.350	1.748	1.014
Cumulative TVE	8.60	13.10	15.70
Pearson Corr	0.922***	0.789***	0.799***
Slope	0.099	0.364	-0.362
Elevation	-0.812***	0.481	-0.090
Aspect	-0.225	0.339	0.320
Soil moisture	-0.635**	0.083	-0.060
Bulk density	-0.144	-0.062	-0.024
Total nitrogen	-0.652**	0.192	0.052
AvP	0.041	-0.048	0.146
Organic matter	-0.231	-0.195	0.148
Electrical conductivity	-0.586*	0.077	-0.176
pH	0.763**	0.058	0.065
Settlement	0.278	0.618**	-0.53
Canopy openness	0.028	0.220	-0.348
Cutting	-0.41	-0.569*	-0.172
Grazing	-0.263	-0.471*	-0.339

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

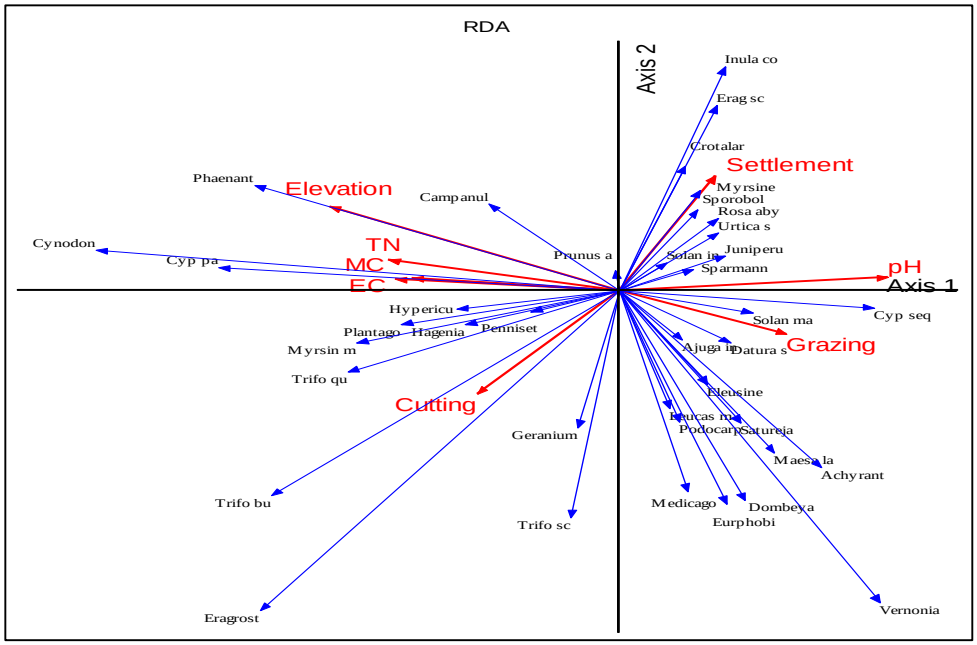


Figure 37. RDA ordination bi-plot of SSB species and environmental variables

Cynodon = Cynodon dactylon; pharan t= cyp pa= Cyperus Pauper; Hypercu = hypercum revolutum; Trifo sc= Trifolium schimperi; inula co= Inula confertiflora; Erag sc= Eragrostis schweinfurthii; crotalar = Crotalaria pycnostachya;Myrsine = Myrsine Africana; Sporobol = Sporobolu pilifenas; Rosa aby= Rosa abyssinica; Urtica s= Urtica simensis; Juniperu= Juniperus procera;sparmann= Sparmannia ricinocarpa; Solan in= Solanum incanum; cyp seq= Cyperus sesquiflorus; Ajuga = Ajuga integrifolia; Eleusin= Eleusine floccifolia; Lucas tr = Leucas martinicensis;Podocarpus = Podocarpus falcatus; Satureja = Satureja abyssinica; Maesa la = Maesa lanceolate; Achyrant = Achyranthes aspera; Dombeya= Dombeya torida; Medicago=Medicago polymorpha; Eurphrbi= Eurphobia dumalis; Vernonia= Vernonia rueppellii; Eragrost = Eragrostis schweinfurthii;Trifo bu = Trifolium burchellianum; Trifo qu= Trifolium quartinianum; Myrsine m= Myrsine melanophloeos; Plantago = Plantago lanceolate; Hagenia = Hagenia abyssinica

4.8.5. Effect of environmental and disturbance factors on woody species richness and diversity in the soil seed bank

The stepwise multiple regression model in GLM was used to explain soil seed bank species richness and diversity as a function of environmental and disturbance factors. The independent variables used for multiple regression analysis showed low inter-correlation. For all models, all the calculated tolerance values were far from 0 (zero) indicating that the assumption of low collinearity among predictor variables was not violated in this analysis (Table 31 and 32). Moreover, multi-collinearity was

checked in multi regression model using variance inflation factors (VIFs, which were low for all variables, i.e., very closer to 1) indicating that the variables were independent (ter Braak and Sˇmilauer, 2002; Lepsˇ and Sˇmilauer, 2003).

Woody species (trees and shrubs) richness and diversity in the soil seed bank were affected both by environmental and disturbance factors. The stepwise multiple regression model revealed that soil moisture and cutting were the two best models explaining the variation in the woody species richness in the soil seed bank. Soil moisture and cutting had significantly affected the woody species richness in the soil seed bank. Jointly, the two predictors had explained 18.9 % of the variation in woody species richness. Soil moisture was the most predictor of variations in woody species richness (R^2adj = 13.1%; $p < 0.034$) followed by tree cutting (R^2adj= 5.8%; $p < 0.048$).

In the present study, soil moisture and cutting were also the two most important factors negatively influencing woody species diversity in the soil seed bank as similar case in species richness. Both factors together explained 19.2 % of the total variations in woody species diversity. Individually, soil moisture and cutting significantly explained 14.3 % ($p < 0.006$) and 4.9 % ($p < 0.046$) variations in woody species diversity of the soil seed bank, respectively. Several past studies showed that soil moisture was one of the most important predictors of seed bank germination (Snyman, 1998; Snyman, 2004a).

Table 31. Multiple Regression Model for woody species richness in soil seed bank

Model	R^2adj.	ΔR^2adj.	SE	β- coeff	Tolerance	*t*	VIF	*p*
Constant				3.331		6.943		0.000
MC	0.131	0.131	0.919	-2.092	0.919	-2.188	1.08	0.034
Cutting	0.189	0.058	0.888	-0.604	0.919	-2.040	1.08	0.048

MC= soil moisture content; t= statistic, VIF= variance inflation factor; SE= standard error; R^2ad= adjusted R-square ΔR^2adj = change of adjusted R^2

Table 32. Multiple Regression Model for woody species diversity in soil seed bank

Model	R^2adj.	ΔR^2 adj.	SE	β- coeff	Tolerance	*t*	VIF	*p*
Constant				1.227		5.084		0.000
MC	0.143	0.143	0.461	-1.122	0.919	-2.334	1.0	0.006
Cutting	0.192	0.049	0.447	-0.286	0.919	-1.921	1.0	0.046

4.8.6. Effects of environment and disturbance factors on herbaceous species (grasses, sedges and herbs) richness and diversity in soil seed bank

Soil pH and total nitrogen were the two most important explanatory variables for herbaceous species richness in the soil seed bank. The stepwise multiple regression model forward selection procedure showed only pH and total nitrogen variables as the best significant models predicting the variations in the herbaceous species richness in the soil seed bank. Both variables together explained 26.5 % of the variation in herbaceous species richness. The variation decomposition indicated that pH negatively and significantly explained (R^2adj = 19.4 %; $p < 0.004$) more variations in herbaceous species richness than the total nitrogen (R^2adj = 7.1%; $p < 0.01$). One of the most important variables for seed bank germination is soil pH (Thanos and Skordilis, 1987; Henig-Server *et al*., 1996). Basto *et al*. (2015) found that decreasing soil pH was correlated with increasing grass seed number in the seed bank. Because acid soils (low pH) are associated with increased seed persistence of herbaceous seed banks via affecting microbial pathogens that act on the physical damage of seeds in the soil seed bank (Basto *et al*., 2015).

The soil seed bank species diversity of the herbaceous species was significantly explained by elevation, settlement and grazing. Jointly, the three factors explained 30.4 % of the total variations of species diversity in the soil seed bank. Grazing pressure was the most significant predictor explaining most variations in the species diversity (R^2adj = 28.2 %; $p < 0.042$). Settlement and elevation explained 1.3 % ($p <$

0.004) and 0.9 % ($p < 0.000$) variations of the soil seed bank diversity in the study area, respectively. Spatial distribution of seedlings in the soil seed bank can also be affected by topography, especially elevation, through its effect on drainage, moisture and nutrient variation (Mamo *et al*., 2012).

Table 33. Multiple Regression Model in herbaceous species richness in soil seed bank

Model	R^2adj.	ΔR^2adj.	SE	β- coeff	Tolerance	*t*	VIF	*p*
Constant			1.859	7.628		4.103		0.000
pH	0.194	0.194	0.258	-0.777	0.872	-3.011	1.147	0.004
TN	0.265	0.071	1.284	3.423	0.872	2.666	1.147	0.010

TN= total nitrogen

Table 34. Multiple Regression Model in herbaceous species diversity in soil seed bank

Model	R^2adj.	ΔR^2adj.	SE	β- coeff	Tolerance	*t*	VIF	*p*
Constant				-1.702		-2.440		0.018
Grazing	0.282	0.282	0.368	0.001	0.748	2.073	1.337	0.042
Settlement	0.295	0.013	0.365	-1.702	0.991	-3.029	1.009	0.004
Elevation	0.304	0.009	0.362	0.001	0.743	4.596	1.347	0.000

4.8.7. Relationships between soil seed bank and standing vegetation

A total of 44 woody species were identified both in the standing vegetation and soil seed banks together. 12 (27 %) species were common to the soil seed banks and standing vegetation. From the twelve species found in common both in the seed bank and aboveground vegetation, seven species were trees (*Dombeya torrida, Hagenia abyssinica, Hypericum revolutum, Juniperus procera, Myrsine melanophloeos, Podocarpus falcatus* and *Prunus Africana)* four species were shrubs (*Inula confertiflora, Rosa abyssinica, Vernonia rueppellii* and *Myrsine africana)* and one species was tree / shrub (*Maesa lanceolata*). The under-representation of these species

in the seed banks makes the restoration of degraded Adaba-Dodola Afromontane forest more difficult to restore based on natural /passive restoration strategy.

Twenty-six woody plant species (13 trees, 11 shrubs, 1 tree/shrub and 1 liana) which were found in the standing vegetation were not represented in the soil seed bank. Similarly, Tekle (2000) reported that more than 30 tree species that were recorded in the standing vegetation did not occur in the seed bank in the Afromontane forest of northern part of Ethiopia. Six shrub species that were not represented in the standing vegetation were recorded in the soil seedbank in the present study. The six shrub species that were not represented in the standing vegetation but recorded in the soil seed bank include *Achyranthes aspera, Crotalaria pycnostachya, Datura stramonium, Solanum incanum, Solanum marginatum* and *Sparmannia ricinocarpa.* There was no tree species represented only in soil seed bank.

68.41 % (i.e., 26 of 38) of the total standing vegetation were not represented by soil seed bank whereas 33.33 % of the total floras in the seed bank were not represented by standing vegetation of this study. The standing tree species which were not represented in the seed bank include: *Rhus glutnosa, Schefflera volkensii, Bersama abyssinica, Schefflera myriantha, Lobelia rhychnchopetalum, Psychotria orophila, Dovyalis abyssinica, Ekebergia capensis, Galiniera saxifraga, Maytenus arbutifolia, Myrica salicifolia, Nuxia congesta* and *Olea europaea.* The woody shrub species that were not represented in the seed bank were *Buddleja polystachya, Carissa spinarum, Discopodium pennlnervium, Dovyalis abyssinica, Galiniera saxifraga, Gnidia glauca, Maytenus undata, Olinia rochetiana, Osyris quadripartite, Rhamnus staddo and Scolopia theifolia.*

Jaccard's coefficient of similarity revealed that the correspondence between species in the standing vegetation and in the seed bank was very low (i.e., 27 %). This

coefficient varied from 0 % similarity in liana species to 50 % similarity in tree/shrubs among the standing vegetation and soil seed banks (Table 35). This result was in accordance with other soil seed bank studies in Ethiopia by Mulugeta and Demel (2006) and Feyera and Demel (2002). Tekle (2000) also found an overall 26 % floristic similarity between the species in the standing vegetation and in the seed bank in northern Afromontane forest of Ethiopia, which was very close value to the current result. Demil and Granstro¨m (1996) also reported very low similarity (16 %) between stand vegetation and soil seed bank in Wendo Genet Afromontane forest of southern Ethiopia. Major and Pyott (1966), Thompson & Grime (1979) and Roberts (1981) mentioned that there was generally a low degree of concordance between the seed bank and the standing vegetation composition. Holmes and Cowling (1997) in South African shrub lands explained the lack of correspondence between the standing vegetation and seed banks.

A low similarity or the lack of correspondence between the seed banks and above-ground vegetation has been reported also in different habitats, like sand dunes (Planisek and Pippen, 1984), grasslands (Funes *et al*., 2003; Koch *et al*., 2011), semi-arid rangeland (Solomon *et al*., 2006), alpine meadows (Ma *et al*., 2010), salt marshes (Erfanzadeh *et al*., 2010) and the lower ranges of the Hyrcanian forest (Esmailzadeh *et al*., 2011). This low similarity indicates that the contribution of the dominant species to the formation of the soil seed bank is of minor importance. In contrast, high similarity between the aboveground vegetation and the soil seed bank has been reported in few only other studies (Shaukat and Siddiqui, 2004). The reason for the disparity between aboveground vegetation and soil seed bank flora may be seeds of the woody plant species in above ground flora germinate immediately after dispersal (have transient seeds), lack of dormancy mechanisms of many woody species to

germinate (Archibold, 1979; Baskin and Baskin, 1998; Sem and Enright, 1996; Tekle, 2000).

Seed or endocarp dormancy of *Juniperus procera* and *Olea europaea* results in slow germination (Jones, 1989; Legesse, 1995). In their seed viability, study of Afromontane tree species in forest soils of Ethiopia, Demel and Granstro¨m (1997) found that there was 37 % viability for *Juniperus procera* and *Olea europaea* after four years of burial, but almost 100% for was recorded for *Acacia abyssinica* viability. Furthermore, *Juniperus procera* has seeds that are predated by animals (McGee & Feller, 1993, Demel & Granstro¨m, 1995) that can also hinder the fast natural regeneration of this tree from the soil seed banks (even if seeds are present). These authors mentioned that woody species with transient seeds would germinate immediately within a few days after dispersal, which is a characteristic of many woody species.

In the present study, the woody species of the soil seed bank showed greater compositional dissimilarity (Jaccard index) with standing vegetation in overall sites. The seed bank of Adaba-Dodola degraded forest contains a relatively low seed emergent density and species richness for woody plants. Because of the low similarity of the soil seed bank with standing vegetation, seed bank alone will not be helpful for restoration of the degraded vegetation (Halassy, 2001; DeVilliers *et al*., 2003). As long as the soil seed bank species were poorly representing the standing vegetation, the species in the forest were vulnerable to elimination from the standing vegetation (Fenner, 1985; O'Connor, 1991). Moreover, the high dominance of annual (pioneer) herbs and grasses and the absence of most dominant perennials trees in the soil seed bank suggested that target species might require active enrichment with adaptable species for further restoration of the degraded forest. The restoration of these species

would be difficult and slow to accomplish if they are destroyed to the worst case than the current condi

Table 35. Number of species in standing vegetation and soil seed bank

Growth form	SV	USV[c]	SSB*	USSB[b]	CSV & SSB[a]	Sj
Trees	20	13	7	0	7	0.35
Shrubs	15	11	10	6	4	0.19
Trees /shrub	2	1	1	0	1	0.50
Liana	1	1	0	0	0	0.00
Total	38	26	18	6	12	0.27[d]*

SV= standing vegetation; SSB= soil seed bank; USV= unique species in standing vegetation; USSB = unique species in soil seed bank; CSV & SSB = common in standing vegetation and soil seed bank; Sj = Jaccard coefficient of similarity; Sj = $a / a + b + c$, where a represents the CSV & SSB, b represents USSB; c represents USV; *= only the woody species is considered for SSB. [d]Mean jaccard similarity value.

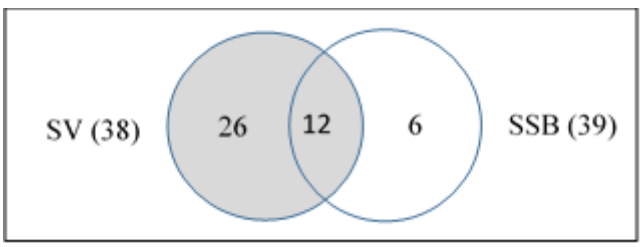


Figure 38. The Venn diagram representation of the total, common and unique species in the standing vegetation (SV) and soil seed bank (SSB) of Adaba-Dodola Afromontane forest

Table 36. List of woody species represented by soil seedbank and aboveground in vegetation communities

Species	Aboveground community				Seedbank community				
	I	II	III	IV	I	II	III	IV	LF
Achyranthes aspera	-	-	-	-	+	-	-	-	S
Allophyllus abyssinicus	+	-	-	-	-	-	-	-	T
Bersama abyssinica	+	-	-	-	-	-	-	-	T
Buddleja polystachya	+	+	-	+	-	-	-	-	S
Carissa spinarum	+	-	-	-	-	-	-	-	S
Crotalaria pycnostachya	-	-	-	-	-	+	-	+	S
Datura stramonium	-	-	-	-	+	-	-	-	S
Discopodium pennlnervium	-	-	-	+	-	-	-	-	S
Dombeya torrida	-	+	-	-	+	-	+	-	T
Dovyalis abyssinica	+	+	-	-	-	-	-	-	S
Ekebergia capensis	+	+	-	-	-	-	-	-	T
Erica arborea	-	+	+	+	-	-	-	-	T/S
Galiniera saxifraga	+	+	+	-	-	-	-	-	S
Gnidia glauca	-	-	-	+	-	-	-	-	S
Hagenia abyssinica	+	+	+	+	+	+	-	+	T
Hypericum revolutum	-	+	+	+	+	+	+	+	T
Inula confertiflora	-	+	+	+	+	+	+	-	S
Juniperus procera	+	+	+	+	+	-	-	+	T
Lobelia rhychnchopetalum	-	+	-	-	-	-	-	-	T
Maesa lanceolata	-	-	+	-	+	-	-	-	T/S
Maytenus arbutifolia	+	-	-	-	-	-	-	-	T
Maytenus undata	+	+	+	-	-	-	-	-	S
Myrica salicifolia	-	+	-	-	-	-	-	-	T
Myrsine Africana	+	+	-	-	+	+	+	-	S
Myrsine melanophloeos	+	+	+	+	-	-	+	+	T
Nuxia congesta.	+	+	+	+	-	-	-	-	T
Olea europaea	+	+	-	-	-	-	-	-	T
Olinia rochetiana	+	+	-	+	-	-	-	-	S
Osyris quadripartite	+	+	+	+	-	-	-	-	S
Podocarpus falcatus	+	+	+	-	+	-	-	-	T
Prunus africana	+	+	-	-	+	-	-	-	T
Psychotria orophila	+	-	-	-	-	-	-	-	T
Rhamnus staddo	+	-	-	-	-	-	-	-	S
Rhus glutjnosa	+	+	-	-	-	-	-	-	T
Rosa abyssinica	+	-	-	-	-	+	-	-	S
Rubus steudneri	+	+	+	-	-	-	-	-	L
Schefflera myriantha	-	+	-	-	-	-	-	-	T
Schefflera volkensii	+	+	+	+	-	-	-	-	T
Scolopia theifolia	+	-	-	-	-	-	-	-	S
Sideroxylon oxyacantbum	+	-	-	-	-	-	-	-	S
Solanum incanum	-	-	-	-	+	-	-	-	S
Solanum marginatum	-	-	-	-	+	+	+	-	S
Sparmannia ricinocarpa	-	-	-	-	+	+	-	-	S
Vernonia rueppellii	+	-	+	-	+	-	-	-	S

+: present in the site; -: absent in the sites; T= Tree; S= Shrub; T/S= Tree/shrub; L =Liana

4.9. CCA-ordination analysis of plant species with environmental and disturbance factors

Plant community distribution in environmental gradients is reflected by physical environments such as topographic, edaphic, microclimatic and historical disturbances (Delcourt *et al.*, 1983; Lima and Zollner, 1996).

In the present study, the relationship of plant species composition with environmental and anthropogenic disturbance variables was assessed using canonical correspondence analysis (CCA). The analysis showed significant effect ($p < 0.005$) of various environmental and disturbance factors on species composition and patterns. As depicted by Table 37 and Figure 39, for the first three axes, the cumulative percentage variance of species-environment relationship was 27 % with eigenvalues of 0.72, 0.21 and 0.15, respectively. The total inertia was 4.0648. The species-environment correlations calculated for the first three axes were 0.96, 0. 84 and 0.86, respectively (Table 37). A Monte Carlo permutation test showed that the species-environment relationships and eigenvalues for the first canonical axis were significant ($p < 0.001$).

The CCA axis 1 (x-axis) had significant ($p < 0.001$) and strong effect on species composition variation and was mainly explained by environmental factors such as elevation ($r^2 = -0.96$), soil moisture ($r^2 = -0.77$), pH ($r^2 = 0.75$), EC ($r^2 = -0.50$) and TN ($r^2 = -0.56$) while the second axis was mainly explained by disturbance factors including grazing ($r^2 = 0.50$), settlement ($r^2 = -0.71$), cutting ($r^2 = 0.55$) and CO (r^2=-0.46) (Table 37 and Figure 39). Considering the strong correlation of both environmental and disturbance factors to the canonical axes, it might be inferred that both environmental and disturbance factors were important in woody species variation and structuring plant communities in Adaba-Dodola Afromontane forest.

Elevation arrows pointed to the left side of the CCA plot along the first axis while pH arrow pointed towards the right side. This implied that there was high pH (low H^+ concentration) at low elevation of the study area that might be due to more salt accumulation in low altitudes (Charan *et al.,* 2013). Figure 39 clearly depicted that the distribution pattern of plant species on the ordination biplot was related to environmental and disturbance gradients whereby species on the left side of the ordination biplot such as *Erica arborea, Hypericum revolutum, Hagenia abyssinica* and *Schefflera volkensii* corresponded to high elevation areas while the species on opposite side in the ordination biplot occurred at lower elevation. Species occurred around the centroid of the axis corresponded to intermediate environmental and disturbance gradients.

Table 37. Relationships of environmental and anthropogenic factors with species and CCA axes (Total inertia = 4.065)

Variables	Axis 1	Axis 2	Axis 3
Eigenvalue	0.80***	0.12	0.096
% of variance explained in species data	17.7	5.2	3.7
Cumulative % variance in species data	17.7	22.9	26.7
Species-environment correlation	0.964**	0.835*	0.860*
Slope	0.119	-0.281	0.247
Elevation	-0.964	-0.205	-0.030
Aspect	-0.030	0.088	0.245
Soil moisture	-0.777	0.183	-0.083
Bulk density	0.281	0.188	-0.395
Total nitrogen	-0.564	0.191	-0.059
Available Phosphorus	0.003	0.309	-0.193
Organic matter	-0.178	0.403	-0.001
Electrical conductivity	-0.495	0.267	0.220
pH	0.752	-0.057	0.218
Settlement / habitation	-0.015	-0.708	0.054
Canopy openness	0.025	-0.462	-0.611
Cutting	-0.103	0.557	-0.176
Grazing	0.501	0.028	0.037

***P< 0.001; Monte Carlo permutation test of 999 runs used for significance

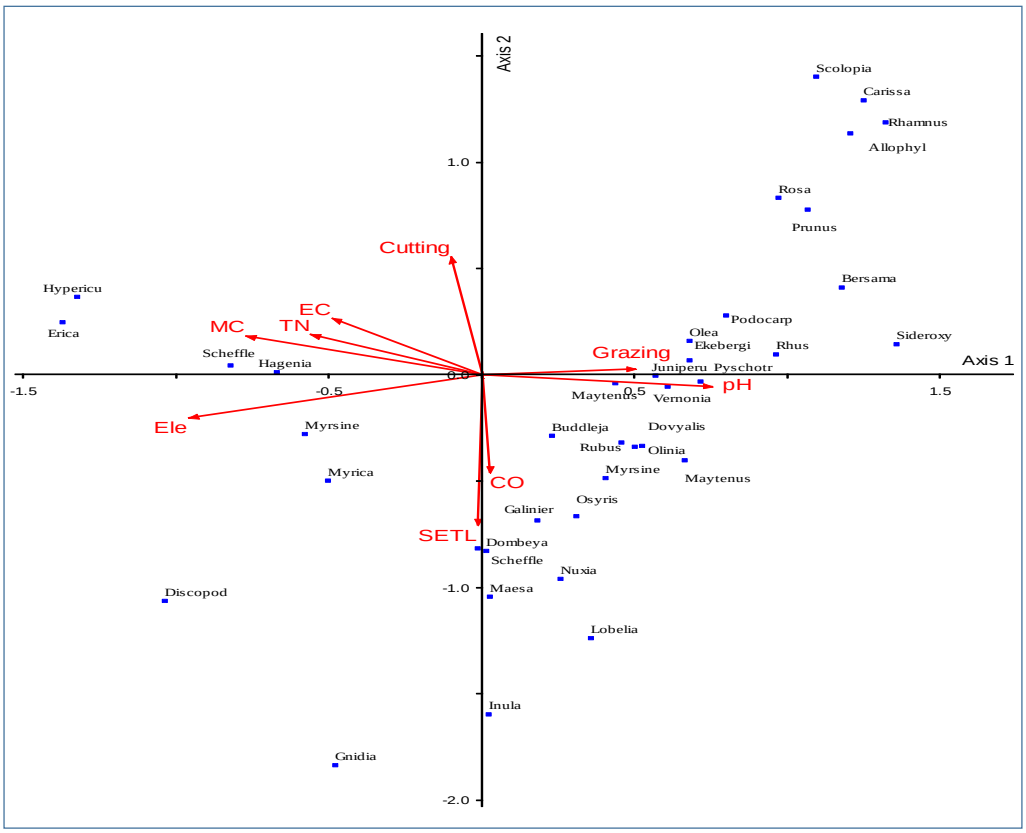


Figure 39. CCA ordination bi-plot of species and environmental variables for whole community and along complete elevation

Hypercum = Hypericum revolutum; Erica = Erica arborea; Scheffle= Schefflera myriantha; Hagenia= Hagenia abyssinica; Myrsine= *Myrsine melanophloeos;* Myrica = *Myrica salicifolia;* Discopod = *Discopodium pennlnervium;* Grindia = *Gnidia glauca;* Inula= *Inula confertiflora ;* Lobelia= *Lobelia rhychnchopetalum;* Maesa= *Maesa lanceolate;* Nuxia= *Nuxia congesta;* Schefle v = *Schefflera; volkensii;* Galinier = *Galiniera saxifrage;* Osysris = *Osyris quadripartite;* Myrsine = *Myrsine africana;* Maytenus u = *Maytenus undata;* Ollinia= *Olinia rochetiana;* Rubus = *Rubus steudneri;* Budelja = *Buddleja polystachya;* Dovylis = *Dovyalis abyssinica;* Maytenus = *Maytenus arbutifolia;* Vernonia = *Vernonia rueppellii;* Juniperus= *Juniperus procera;* Pyschotr = *Pyschotria orophila;* Rhus= *Rhus glutjnosa;* Ekebergi= *Ekebergia capensis;* Sideroxy= *Sideroxylon oxyacantbum;* Podocarp = *Podocarphus falcatus;* Olea = *Olea europaea;* Bersama = *Bersama abyssinica; Prunus = Prunus africana;* Rosa= *Rosa abyssinica;* Allophyll= *Allophyllus abyssinicus;* Rhamnus = *Rhamnus staddo;* Carrisa = *Carissa spinarum;* Scolopia= *Scolopia theifolia*

Table 38. Pearson correlation coefficient between dependent and independent variables

Variables	Slope	Elev	Aspect	MC	BD	TN	AvP	OM	EC	pH	SETL	CO	Cutting	Grazing	S	E	H	D
Slope	1																	
Elev	-0.06	1																
Aspect	-0.05	0.02	1															
MC	-0.13	0.73**	0.05	1														
BD	-0.01	-0.31*	-0.05	-0.27*	1													
TN	0.04	0.58**	0.03	0.44**	-0.29*	1												
AvP	-0.05	0.03	0.05	0.11	-0.25*	0.36**	1											
OM	0.2	0.16	-0.02	0.21	-0.21	0.49**	0.42**	1										
EC	-0.05	0.52**	0.07	0.57**	-0.25*	0.47**	0.42**	0.28*	1									
pH	0.2	-0.69**	0.1	-0.57**	-0.03	-0.42**	0.23	-0.13	-0.17	1								
SETL	0.07	0.17	-0.19	0.09	-0.41**	-0.08	0.03	-0.25*	0.09	0.09	1							
CO	0.06	0.05	-0.26*	-0.15	0.05	0.02	-0.18	-0.03	-0.12	-0.06	0.22	1						
Cutting	0.1	-0.36**	0.14	0.09	0.17	0.17	-0.08	0.31*	0.09	-0.25*	-0.35**	0.14	1					
Grazing	0.07	-0.53**	0.18	-0.37**	0.05	-0.22	0.11	-0.11	-0.29*	0.47**	0.08	0.09	0.01	1				
S	0.18	-0.50**	-0.04	-0.48**	0.04	-0.37**	-0.08	-0.24	-0.30*	0.51**	0.32**	0.28*	-0.22	-0.29*	1			
E	0.01	-0.09	0.04	-0.09	-0.06	-0.31*	-0.04	-0.2	0.02	0.27*	0.26*	-0.26*	-0.54**	0.01	0.30*	1		
H	0.15	-0.44**	-0.05	-0.37**	0.07	-0.45**	-0.11	-0.25*	-0.22	0.51**	0.32**	0.07	-0.41**	-0.23	0.78**	0.72**	1	
D	0.11	-0.33**	-0.02	-0.32**	-0.02	-0.40**	-0.03	-0.23	-0.16	0.48**	0.30*	-0.03	-0.53**	0.17	0.69**	0.85**	0.90**	1

** Correlation is significant at the 0.01 level; * Correlation is significant at the 0.05 level; SETL= settlement; Elev= Elevation; MC= moisture content; BD= Bulk density; TN= Total nitrogen; AvP= Available phosphorus, OM= organic matter; EC= Electrical conductivity; CO= Canopy openness; S= richness, E= evenness; H Shannon index; D= Simpson index.

4.10. Effects of environmental and disturbance factors on species composition

4.10.1. Species composition variation partitioning in the entire community

During the analysis of the relative influence of set of variables, a pairwise Pearson correlation and variance inflation factor (VIF) tests were done using GLM and RDA/CCA (in CANOCO) models to detect the high collinearity between variables in each set of environmental and disturbance variables (Quinn and Keough, 2002). Accordingly, the high collinear variables were removed at each analysis. The CCA-based correlation and biplot results showed that the gradients of species composition in the Adaba-Dodola forest were strongly related to the environmental and disturbance descriptors that were included in the study. The disturbance and environmental factors together explained 44.26% of species composition variation in the entire community (Table 39). Pure environment [a], pure disturbance [c] and shared disturbance and environmental factors [b] accounted for 30.26%, 7.63% and 6.37% of the total variances explained (TVE) in species composition, respectively (Table 39 and Figure 40e). Both fractions of environment [a+b] and disturbance factors [b+c] explained significant portions of the total variations (p [a+b] = 0.005; TVE [a+b] = 36.41; p [b+c] = 0.005; TVE [b+c] =14) at 999 permutations). Pure environmental factors [a] explained significantly more variations (p [a] = 0.005; TVE [a] = 30.26) than pure disturbance factors [c] (p [b+c] = 0.005; TVE [c] =7.63).

The canonical (CCA) ordination results indicated that environment was the most important predictor than disturbance predictor in explaining the variation in the species composition and patterns when the whole elevation gradient was considered. The CANOCO based variation partitioning model further confirmed the dominant role played by environment as a driver of species composition and distributions with the

pure environmental fraction constituting more than 68 of the total variance explained (TVE) by the joint predictors (Table 39). Our results agreed with many previous studies, which had shown that environment is strong control of landscape and local-scale species distributions and compositions in forests (Motzkin *et al*., 1999; Svenning and Skov, 2002; Gilbert and Lechowicz, 2004; Graae *et al*., 2004; Borchsenius *et al*., 2004; Thomsen *et al*., 2005). Because environment consits of a couple of many physical gradients that affect community composition as compared to the anthropogenic disturbance (Fonda and Bliss, 1969; delMoral and Watson, 1978).

From the fractions of environmental factors [a+b] considered, elevation explained significantly the largest portion of variations in species composition (TVE= 16.73 %; p = 0.005) which represented about half (46 %) of the total variations explained by fraction of the environmental factors. Elevation still explained significantly (TVE= 12.79 %; p = 0.005) the largest portion of variation even when effects of disturbance variables were removed as covariance data from the canonical analysis model. This is because in mountainous regions, elevation is considered as the primary physical gradients affecting community composition due to the fact that elevation influences temperature and precipitation, which in turn affects the soil moisture and exposure to solar radiation (Fonda and Bliss, 1969; delMoral and Watson, 1978). Soil moisture, TN and EC significantly explained 3.20 % (p = 0.005), 1.97% (p= 0.040) and 11.97% (p = 0.030) variations in species composition, respectively. Peet (1978) and deLafontaine (2007) reported similar results that the soil moisture was an important factor affecting the pattern of vegetation. Baniya *et al.* (2010) also observed positive linear trend in species composition and richness of different trees with soil moisture.

The distribution of species such as *Hagenia abyssinica*, *Schefflera volkensii*, *Erica arborea* and *Hypericum revolutum* were positively associated with these soil factors whereas species such as *Myrsine melanophloeos*, *Buddleja polystachya*, *Vernonia rueppellii*, *Ekebergia capensis* and *Dovyalis abyssinica* were negatively associated with soil moisture, TN and EC soil factors (Figure 39 and Table 39). Topographic (elevation, slope and aspect) and edaphic factors, respectively, explained about 57 % and 43% of the total fractions of variations during overlapping (tandem) effects of environment with disturbances. However, when the influence of disturbance factors removed, 54 % and 46% of the explained variations by environment were contributed by topographic and edaphic factors, respectively.

Generally, when the entire community along a complete elevation band was considered, environment had significantly (p = 0.005) better explained the variations as a pure component [a] or as an overlapping effect [a+b]. The amount of unexplained variation [d] was fairly high (55.74%) as some residual drivers for the variations are unlikely difficult to determine. Therefore, 55.74 % of total variations contributed in structuring tree species composition could not be explained by the measured variables. These high residual can be expected as there could be several environmental heterogeneities existing within a wide range of elevation due to environmental factors or biotic disturbances or variations due to competition that determine the species distribution, stochastic processes and ecological drift and dispersal limitations (Grubb, 1977).

Table 39. Species composition variation partitioning in the whole community (Total inertia (TI) =4.065)

Predictors	Eigenvalues	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	1.48	36.41	0.005	
Elevation	0.68	16.73	0.005	3.88
Moisture content	0.15	3.69	0.005	2.82
Slope	0.11	2.71	0.005	1.21
Total nitrogen	0.10	2.46	0.005	2.36
EC	0.08	1.97	0.015	2.30
Available P	0.09	2.21	0.035	1.99
Bulk density	0.08	1.97	0.025	1.44
OM	0.08	1.97	0.050	1.65
Aspect	0.06	1.48	0.215	1.04
Disturbance variation: [b+c]	0.567	14.00	0.005	
Grazing	0.22	5.41	0.005	1.01
Canopy openness	0.14	3.44	0.005	1.08
Cutting	0.13	3.20	0.005	1.24
Settlement	0.08	1.97	0.150	1.29
Pure environmental variation: [a]	1.23	30.26	0.005	
Elevation	0.52	12.79	0.005	4.82
Moisture content	0.13	3.20	0.005	3.08
Slope	0.08	1.97	0.015	1.48
Total nitrogen	0.08	1.97	0.040	2.48
Available P	0.08	1.97	0.010	2.19
EC	0.08	1.97	0.030	2.41
Bulk density	0.07	1.72	0.070	1.89
Aspect	0.07	1.72	0.090	1.34
OM	0.06	1.48	0.105	2.14
Pure disturbance variation: [c]	0.31	7.63	0.005	
Canopy openness	0.11	2.71	0.005	1.36
Cutting	0.08	1.97	0.010	1.52
Grazing	0.06	1.48	0.150	1.71
Settlement	0.06	1.48	0.150	2.19
Total variation: Y = a+b+c		44.26		
Shared Variation: [b]		6.37		
Residual: [d] = 100-[a+b+c]		55.74		

EC= electrical conductivity; OM= organic matter

4.10.2. Species composition variation partitioning in *Podocarpus falcatus-Olea europea* forest community

This community was generally located at the low elevation zone of the study area. The disturbance and environmental factors together explained 66% of species composition variations in this community (Table 40). Both fractions of environment [a+b] and disturbance [b+c] factors explained significant portions of the variation (p [a+b] = 0.005; TVE= 44 %; p [b+c] = 0.005; TVE= 30 %). Significantly, more species composition variation was explained by fraction of environmental factors [a+b] than by the fractions of disturbance factors [b+c] ($p < 0.005$). Pure environment [a], pure disturbance [c] and shared disturbance and environmental factors [b] or [a∩b] accounted for 36 %, 22 % and 8.5 % of the total variations, respectively (Table 40 and Figure 40 a). Both pure environment [a] and pure disturbance [c] explained significant portions of the total variations (p[a] = 0.005; TVE = 36 %; p[c] = 0.005; TVE = 21.5). Pure environmental factors [a] explained significantly more species variation than pure disturbance [c] factors ($p < 0.005$) (Table 40**)**.

The total variation explained by each set of predictor was decomposed into component variables under each predictor to identify the variables having high power of influence on the species composition. During environmental data set decomposition, elevation, soil moisture and OM had significantly influenced the species composition when the disturbance effect was not partialled out. However, the proportion of variations explained by elevation was declined and became insignificant when the disturbance factor was partialled out from environmental factors (p = 0.370; TVE = 4 %), whereas the soil moisture and OM were still significant. This implied that the explaining power of elevation was inflated due to the confounded effect of disturbance factors. Soil moisture and OM were the most important environmental variables

explaining the variation of species composition in this community during isolation of environmental factors. Most *Podocarpus falcatus-Olea europea* communities, for example, such as *Pyschotria orophila, Ekebergia capensis, Myrsine melanophloeos, Vernonia rueppellii, Sideroxylon oxyacantbum, Buddleja polystachya*, *Podocarpus falcatus* were distributed in low soil moisture and low soil organic matter. The high anthropogenic impact existing in the site (tree cutting, human settlement, grazing) removed the litter cover of the soil that might be the reason for low soil moisture and OM at this site. In agreement with this result, Lopez-Martınez *et al* (2013) reported that organic matter had the largest influence on forest species composition. Because organic matter contributes to soil fertility by increasing water retention capacity and nutrient availability to the plants through catalyzing the cationic exchange activities (Guariguata and Ostertag, 2001). Ekeke and Okokwu (2013) stated that the lower organic matter content of low land soils can be attributed to low plant cover, as vegetation removal, due to anthropogenic factors such as collection of fuel wood, encroachment by agriculture and tree falling for construction, which in turn affects species composition.

From disturbance factors, cutting and settlement significantly explained the largest proportion of variation when the confounding effects of environmental factor was partialled out (cutting: $p < 0.005$; TVE= 16%; settlement: $p < 0.005$; TVE= 8%) or not partialled out (cutting: $p < 0.005$; TVE= 8%; settlement: $p < 0.025$; TVE= 5%). This could be attributed to the high density of tree stumps (i.e., high tree felling) and very proximal human settlement to sampled plots in this forest community which might have negatively influenced the vegetation. The strong joint and the fairly shared effects of disturbance and environmental factors in this community (66% vs 8.5 %) also indicated that their effects on species composition were dependent. This result

suggests the incorporation of disturbance factors along with environmental factors is crucial for quantification of the real drivers of species composition patterns.

There was also an evidence of the influence of canopy opening on floristic variation in this vegetation community. The opening of canopy might influence the germination and growth of forest species (Paz and Martı´nez-Ramos, 2003). Canopy openness is a key variable influencing species composition since it determines the amount of light that reaches the underground vegetation (Barton *et al*., 1989). Species such as *Galiniera saxifraga, Dombeya torrida, Nuxia congesta* and *Maesa lanceolata* were distributed associating with high canopy openness. This species may be shade intolerant.

Table 40. Species composition variation partitioning in *Podocarpus falcatus-Olea europea* forest community (TI= 1.00)

Predictors	Eigenvalues	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.44	44	0.005	
Elevation	0.10	10	0.005	2.11
Moisture content	0.07	7	0.015	1.45
OM	0.05	5	0.015	1.86
EC	0.05	5	0.085	6.58
Available P	0.04	4	0.325	3.11
pH	0.03	3	0.405	3.47
Bulk density	0.03	3	0.410	1.86
Slope	0.03	3	0.630	2.35
Total nitrogen	0.02	2	0.790	3.05
Aspect	0.02	2	0.855	1.44
Disturbance variation: [b+c]	0.30	30	0.005	
Cutting	0.16	16	0.005	1.67
Settlement	0.08	8	0.005	1.74
Canopy openness	0.03	3	0.470	1.18
Grazing	0.03	3	0.525	1.17
Pure environment: [a]	0.356	36	0.035	
Moisture content	0.05	5	0.045	3.75
OM	0.04	5	0.021	4.76
Bulk density	0.05	5	0.110	2.29
EC	0.05	5	0.050	7.81
Aspect	0.04	4	0.190	2.20
Available P	0.03	3	0.230	4.51
Elevation	0.03	3	0.370	4.51
Total nitrogen	0.03	3	0.415	3.47
pH	0.02	2	0.635	2.26
Slope	0.02	2	0.720	2.74
Pure disturbance: [c]	0.215	22	0.005	
Cutting	0.08	8	0.005	3.36
Canopy openness	0.06	6	0.025	2.44
Settlement	0.05	5	0.050	5.57
Grazing	0.02	2	0.675	2.19
Total variance explained: a+b+c		66		
Shared variance: [b]		8.5		
Residual Variance: [d] = 100-[a+b+c]		34		

4.10.3. Species composition variation partitioning in *Juniperus Procera-Galiniera saxifraga* forest community

The variance partitioning for disturbance and environmental data set and their components were depicted in Table 41. This community was generally occurred at the middle elevation zone of the study area where the climatic variables are supposed to be optimum for tree growth and development. This community was also characterized with less tree felling and grazing /browsing practices by the local dwellers as compared to the other communities. At optimum climatic conditions, especially at optimum temperature and rainfall, vegetative development and growth increase to optimum level (Hatfield and Prueger, 2015). In the community, the disturbance and environmental variables jointly explained 87% of the variations in species composition. Environmental data set had accounted for significant variation in species composition both as an overlapping effect (TVE =56 %; $p < 0.005$) and as a pure effect (TVE= 55%; $p < 0.015$). However, disturbance data set had no significant effect on the variation of the vegetation pattern in this community (Table 41).

The variations explained due to disturbance data set were small compared to that of the environmental factors, suggesting that the impact of anthropogenic disturbance on this vegetation community might be low. The reason for non-significant influence of anthropogenic disturbance factors might be due to the fact that this forest community experienced less tree cutting and grazing / browsing and located at large geographical distance from village as compared to the other forest communities. Similar result was also reported by Thompson *et al*. (2002) that the human pressure on forest is determined based on the proximity of the human settlements to the forest. The human driven impacts are more localized in the scale of operation and systematic in occurrence as compared to the environmental variables (Thompson *et al*., 2002). This

result was in agreement with Popradit *et al.* (2015) who reported that tree species composition was significantly different depending on the distance from the village boundaries whereby the numbers and composition of woody plant species significantly changed with the distance from the village boundaries toward the forest. Moreover, this forest community was located in more rough terrain (50% sloppy) than the rest communities. This might also reduce the anthropogenic disturbance due to an uneasy accessibility of the site for human and livestock disturbances.

Similarly, the variance explained by edaphic variables was not statistically significant in this community. The optimum values observed for some soil nutrients in this community might have contributed for weak local-scale impact of soil factors on woody vegetation composition and distribution (Allen *et al*., 1991). When the effect of disturbance (covariate) was partialled out (removed) by CANOCO model, OM had explained 14 % of the variations of species composition. However, with the presence of effect of disturbance as a covariate, the explaining power of OM decreased to 11%. In the contrary, the opposite trend was observed in elevation and total nitrogen in the presence of covariate effect (Table 41). This implied that disturbance could change the environmentally structured patterns of species composition by imposing its confounding effect on the explaining power of environmental factors.

In agreement with the current argument, Carpenter (2005) and Marini *et al.* (2009) stated that the environmental heterogeneity due to anthropogenic effect is important in controlling vegetation pattern (Huston, 1994). The omission of potentially important components of human impact on tree species change might draw wrong conclusion about the mechanisms underlying the observed species–elevation relationship (Marini *et al*., 2011). The variances explained by environmental and disturbance components in this community were statistically non-significant except

for the variance explained by the elevation. This meant that elevation appeared as the most important significant (p = 0.010; TEV = 24 % in [a+b]; p= 0.045; TVE = 21% in [a]) factor accounting for variation in species composition.

Table 41. Species composition variation partitioning in *Juniperus procera-Galiniera saxifraga* forest community (TI= 1.00)

Predictors	Eigenvalues	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.558	56	0.005	
Elevation	0.24	24	0.010	1.33
Bulk density	0.14	14	0.195	1.59
OM	0.11	11	0.225	2.13
Total nitrogen	0.07	7	0.600	1.67
Disturbance variation: [b+c]	0.32	32	0.225	
Cutting	0.16	16	0.235	1.21
Grazing	0.10	10	0.485	1.04
Settlement	0.07	6	0.715	1.26
Pure environment: [a]	0.547	55	0.015	
Elevation	0.21	21	0.045	2.06
Bulk density	0.15	15	0.150	4.27
OM	0.14	14	0.145	3.32
Total nitrogen	0.05	5	0.585	2.02
Pure disturbance: [c]	0.311	31	0.350	
Cutting	0.14	14	0.190	2.54
Settlement	0.06	6	0.565	3.04
Grazing	0.11	11	0.275	1.14
Total variation: Y = a+b+c		87		
Shared variation: [b]		1		
Residual fraction: [d]		13		

4.10.4. Species composition variation partitioning in *Myrsine melanophloeos-Hagenia abyssinica* forest community

This community generally occupied from middle to high elevation zone of the study area. In this community, the disturbance and environmental variables jointly explained 93% of the total variations in species composition. The fraction of environment without factoring out the effect of disturbance had explained 79% of the variation in the species composition (Table 42). However, after factoring out the effect of the disturbance, the pure environment [a] contributed for 37 % of the variations. This showed that 42 % of the variation was overlapped by both data sets for explaining the species composition. Fraction of disturbance [a+b] contributed for 56 % of variations in species composition and 14% as a pure effect [c]. There was large value for shared variation (42 %) in this community that revealed the two sets of variables had redundantly affects the species composition, especially disturbance did not explain large unique variation in species composition. The effect of pure disturbance was small and non-significant compared to that of the environmental factors, suggesting that the anthropogenic effect was low as compared to environmental effect in this vegetation community, even though pure effects of both factors were not significant. That means they significantly affect the species composition when they act as a covariate (Table 42).

Table 42. Species composition variation partitioning in *Myrsine melanophloeos-Hagenia abyssinica* forest community (TI= 1.00)

Predictors	Eigenvalues	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.789	79	0.005	
Elevation	0.37	37	0.005	1.42
Slope	0.17	17	0.005	2.52
OM	0.12	12	0.125	3.13
Bulk density	0.11	11	0.120	1.61
EC	0.02	2	0.785	2.89
Disturbance variation: [b+c]	0.558	56	0.045	
Settlement	0.31	31	0.025	2.07
Cutting	0.09	9	0.655	1.37
Grazing	0.09	9	0.700	1.04
Canopy openness	0.07	7	0.675	1.64
Pure environment: [a]	0.372	37	0.140	
Elevation	0.27	27	0.140	3.64
Bulk density	0.10	10	0.400	1.60
Pure disturbance:[c]	0.142	14	0.325	
Cutting	0.09	9	0.350	2.74
Settlement	0.05	5	0.575	1.90
Total variance explained: Y = a+b+c		93		
Shared variation: [b]		42		
Residual variation: [d]		7		

TVE= Total variance explained; VIF= variance inflation factor

4.10.5. Species composition variation partitioning in *Erica arborea-Hypercum revolutum* forest community

In this vegetation, 77 % of variation in community composition was accounted by both data sets (Table 43). The environmental and disturbance fractions accounted for 58 % (p= 0.040) and 22% (p= 0.470) variations, respectively. The unique variations explained by environment and disturbance predictors were 55 % (p = 0.005) and 19% (p = 0.08), respectively. Elevation, total nitrogen and EC had significantly explained the variations in species composition. The high total soil nitrogen in this community might affect plant species and composition through bosting some group of

plants by creating high potential competitive exclusion of the less competent species from the community (Hofmeister *et al*., 2009; Mölder and Schneider, 2011).

Table 43. Species composition variation partitioning in Erica *arborea-Hypercum revolutum* forest community (TI= 1)

Predictors	Eigenvalues	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.58	58	0.040	
Elevation	0.15	15	0.015	4.57
Total nitrogen	0.13	13	0.025	3.00
EC	0.08	8	0.045	2.18
Available P	0.06	6	0.155	2.48
Slope	0.05	5	0.335	2.29
Aspect	0.05	5	0.260	1.54
OM	0.03	3	0.405	2.07
Bulk density	0.03	3	0.590	2.44
Disturbance variation: [b+c]	0.22	22	0.470	
Canopy openness	0.15	15	0.060	1.15
Cutting	0.04	4	0.505	1.05
Grazing	0.02	2	0.755	1.21
Settlement	0.01	1	0.925	1.24
Pure environmental variation: [a]	0.55	55	0.005	
Aspect	0.15	15	0.005	1.24
EC	0.14	14	0.010	1.22
Total nitrogen	0.09	9	0.040	1.05
Available P	0.07	7	0.050	1.21
Bulk density	0.03	3	0.495	1.05
Slope	0.03	3	0.29	1.21
Elevation	0.02	2	0.570	1.24
OM	0.02	2	0.850	1.23
Pure disturbance variation: [c]	0.190	19	0.080	
Cutting	0.07	7	0.080	2.45
Canopy openness	0.06	6	0.145	2.18
Grazing	0.05	5	0.250	2.48
Settlement	0.02	2	0.715	2.29
Total variance explained: Y = a+b+c		77		
Shared variation: [b]		3		
Residual variation: [d]		23		

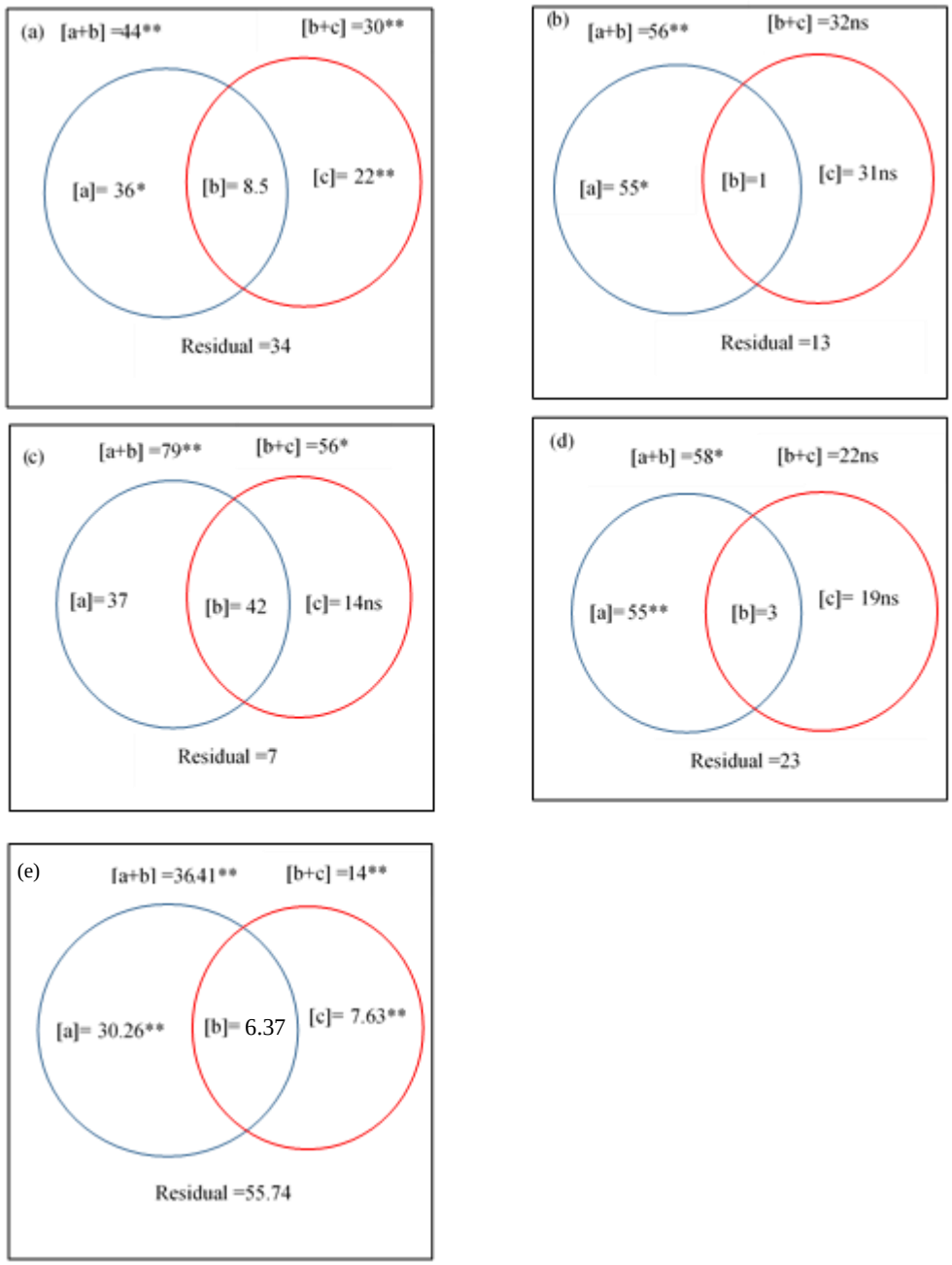


Figure 40. Summary of the variation partitioning Venn diagram of woody species composition

Summary of the Variation partitioning Venn diagram of woody species composition explained by environmental and disturbance fractions (a) *Podocarpus falcatus-Olea europea* (b) *Juniperus procera-Galiniera saxifrage* (c) *Myrsine melanophloeos-Hagenia abyssinica* (d) *Erica arborea- Hypercum revolutum* (e) Whole community along complete elevation. * p <0.05; ** p < 0.01; *** p< 0.001; ns = non-significant; [a+b] = environmental fraction; [b+c] = disturbance fraction; [a] = pure effect of environment; [b] = shared variation; [c] = pure effect of disturbance

4.11. Effects of environmental and anthropogenic factors on species richness and diversity

Diversity and richness regressed against elevation to observe their pattern along the complete elevation gradient. All diversity indices showed gradual change with the change of elevation. Regression model showed a significant and positive quadratic relation ($r^2 = 0.36$; $p = 0.006$) of species richness with elevation. Similarly, species diversity and elevation ($r^2 = 0.47$; $p = 0.001$) and Simpson's index and elevation ($r^2 = 0.47$; $p= 0.001$) exhibited significant relationships (Figure 41). The maximum values were recorded at middle elevation (about 2900 m). Low values for species richness (S), Shannon diversity (H) and Simpson index (D`) were recorded at the higher and lower elevation zones. Species richness and diversity followed a hump-shape pattern and monotonically decreased towards the peak of elevation. This study was consistent with other studies where species richness and diversity decreased monotonically after peak at mid elevation along elevation gradients (Rahbek, 1995). The mid elevation hump-shape pattern in this study also confirmed the previous studies by Friis (1992) in other forest of Ethiopia, by Mwaura & Kaburu (2009) in mountain forest of Kenya, by Zhao & Fang (2006) in China and by Oommen and Shanker (2005) in western Himalayas of India.

The decline of species richness at higher elevations might be attributed to the decline of energy (Rahbek, 1995). Hemp (2006) reasoned out that the mid-elevation peak richness and diversity could be attributed to the optimum climatic conditions at mid elevation allowing many species to coexist. Grace (1999) and VanderMeulen *et al*. (2001) also stated that intermediate environments often contain more species because more species are able to adapt to life in intermediate environments than in extreme environments. Castro *et al*. (2002) in their community richness analysis

indicated that the mid elevation could serve as a transitional zone where it can be a suitable microenvironment (especially, climatic conditions) for many species to coexist. This is because of the fact that many species are able to adapt to life in intermediate environments than in extreme environments (Grace 1999).

The mid elevation maximum richness and diversity pattern was presumed to be emanated from many factors as indicated by variation partitioning models. The RDA variance partitioning model detected that disturbance factors had less impact on both species richness and diversity in mid elevation communities probably due to the less anthropogenic activities of the site. The ANOVA in GLM model analysis and descriptive statistics also confirmed that there were less cutting, grazing/ browsing and human settlement effects in middle elevation forest community. The high topographic roughness (steep and undulating slope) recorded in this forest community site might have also limited the ease accessibility of the forest for anthropogenic activities. The descriptive statistics also indicated that there were intermediate records of soil pH and soil moisture in this vegetation community as compared to the rest communities which in turn might have also favored for the increase of species richness and diversity in this site.

At low elevation, the variance partitioning model indicated that pure anthropogenic activities exerted significant ($p < 0.005$) effect on the species diversity while pure environmental factor did not have significant effect on species diversity. Cutting disturbance had the most pronounced effect on species diversity at low elevation. Therefore, effect of disturbance might be the main reason for the decline of species diversity at low elevation.

However, the reasons for the decline of diversity at the upper elevation zone might be mainly related to environmental factors rather than the disturbance activities.

The multivariate analysis models confirmed that only pure environmental factors had significant contribution for the decline of species diversity. The high total soil nitrogen might have a declining effect on species richness through boosting certain highly competitive plants that weakened, suppressed and excluded the less competent species.

Our results indicated a weak linear decreasing pattern of evenness with elevation but the evenness was so markedly declined at the peak elevation. The current study put forward that the exclusive dominance of *Erica arborea* at the peak elevation of this study area could be the reason for the sharp decline of an evenness. Low species evenness arises due to the dominance of one or few species (Feyera, 2006). The low evenness at the highest elevation site of this study implied that high elevation areas need to be considered as one of the conservation sites (Feyera, 2006).

A positive relationship between species richness and diversity with soil pH was observed. The maximal species richness and diversity were recorded at intermediate soil pH sites. This result was in agreement with Grime (1979) who reported that species richness and diversity increased linearly with the increase in soil pH. Grime (1973) reported the maximum number of species at a soil pH of 6.1- 6.5 with declining species richness towards both acidic and alkaline soils. He concluded that few species are adapted nutritionally to exploit highly acidic or alkaline soils. In agreement with Grime (1973), in our study we also observed the maximum species richness and diversify at about pH of 6-7. Vetaas (1997) found that vascular plant richness was positively related to pH in the Himalayas. Soil moisture was also an important factor affecting the pattern of richness and diversity (deLafontaine and Houle, 2007). Bhattarai and Vetaas (2003), observed a positive linear trend in species richness with moisture. However, in this study, the quadratic relationship of species

richness and diversity with soil moisture was observed where optimum diversity and richness were recorded at the intermediate soil moisture.

But the species richness and diversity were observed decreasing with increasing total nitrogen (Figure 43c & d). Similarly, Dupré *et al*. (2002) reported the increased soil nitrogen content usually reduces the richness of vascular plants. This might be due to positive effect of nitrogen on certain highly competitive plants that competitively excluded the weaker species (Hofmeister *et al*., 2009). Nitrogen enrichment on species richness is also mediated through increased net primary productivity and resulting competition for light (Hautier *et al*., 2009; Borer *et al*., 2014b) or random losses of less abundant species (Suding *et al*., 2005; Yang *et al*., 2015). Other important process related to N enrichment that can lead to species loss are soil acidification (Horswill *et al*., 2008; Maskell *et al*., 2010) and resulting in the mobility of soil Al^{2+} or Mn^{2+} (De Graaf *et al*., 2009; Tian *et al*., 2016). Nitrogen addition can have negative effects through both eutrophication and acidification, which can significantly and independently contribute to species loss (Grace, 2001; Dupré *et al*., 2010; McClean *et al*., 2011).

The overall human impact (cutting, settlement and grazing) was larger in the lowlands and decreased almost monotonically with increased elevation, and the lowest human disturbance was observed at mid elevation (Figure 44a). Similarly, Nogués-Bravo *et al.* (2008) also mentioned that worldwide, human activities generally affected the lower and upper slopes more than the mid-altitudinal habitats.

The deforestation and grazing impact were most intensive in areas where human settlement was very close to the forest patches, particularly in low elevation areas of the present study. According to the current study, the less steepness of the slope of the low elevations (Figure 42e) was one of the decisive environmental factors

that associated with human settlement and grazing impacts in the forest areas. In agreement with this study, Nogués-Bravo *et al.* (2008) also stated that the most suitable area for human settlement usually had lower topographic irregularity. Therefore, lowest species richness and diversity were found in warm and relatively disturbed lowlands (Figure 44a and Figure 42a &b).

Moving upwards elevation, the greatest species richness and diversity (Figure 41a & b) were found in forest-dominated mid-elevations where there were maximum topographic irregularities (steep slope) (Figure 42e), less disturbance index (Figure 44a), medium temperature (Figure 42c), medium soil moisture (Figure 42b), medium pH (Figure 44 d) and medium total nitrogen (Figure 42a) were available. At high elevations, where temperature is low and precipitation is high, relatively, there were low species richness and diversity. Besides the low temperature, edaphic factors such as high nitrogen, low pH and high soil moisture had likely contributed for the decline of species diversity and richness in the high elevation areas. Grime (1973) confirmed that there are maximum number of species at the intermediate soil pH of 6.1- 6.5 with a decline of species richness towards both acidic and alkaline soils.

The analysis of separate elevational intervals at community level based on the multivariate models also shed light on their relative importance of disturbance and environmental factors. The decline of species diversity within lowlands was mainly related to anthropogenic disturbance whereas the decline of diversity within high-elevation areas was mostly related to environmental constraints (climatic and edaphic). According to Horswill *et al*. (2008) and Maskell *et al*. (2010), nitrogen enrichment can lead soil acidification which can be resulted in species loss. Moreover, Dupré *et al*. (2002) noted the increased soil nitrogen content usually reduces the richness of

vascular plants due to positive effect of nitrogen on certain highly competitive species which can suppress and remove the less competent species.

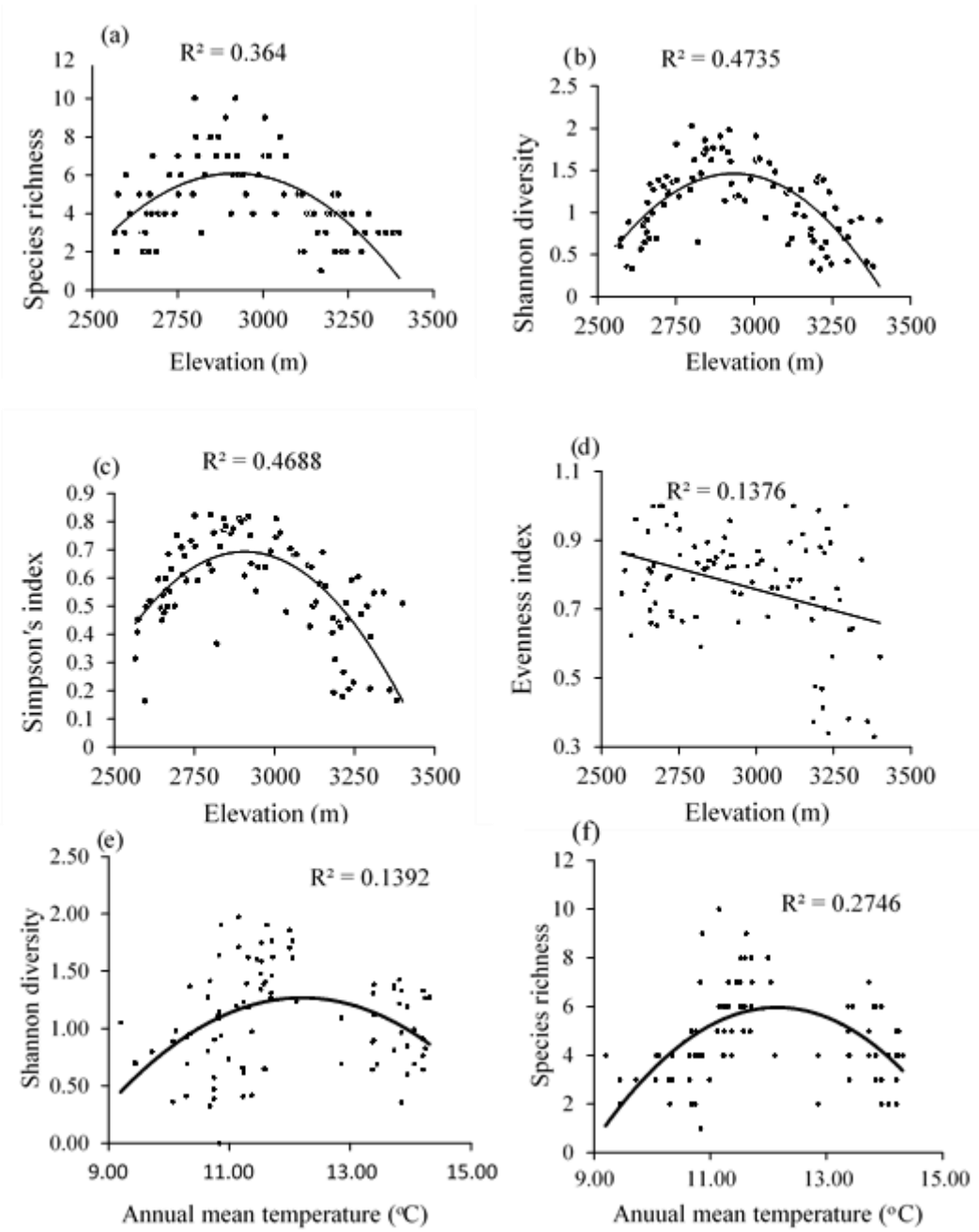


Figure 41. (a) Species richness (b), species diversity, (c) Simpson's and (d) evenness index along elevation gradient and (e) species diversity and (f) species richness relationship with temperature in Adaba-Dodola Afromontane forest

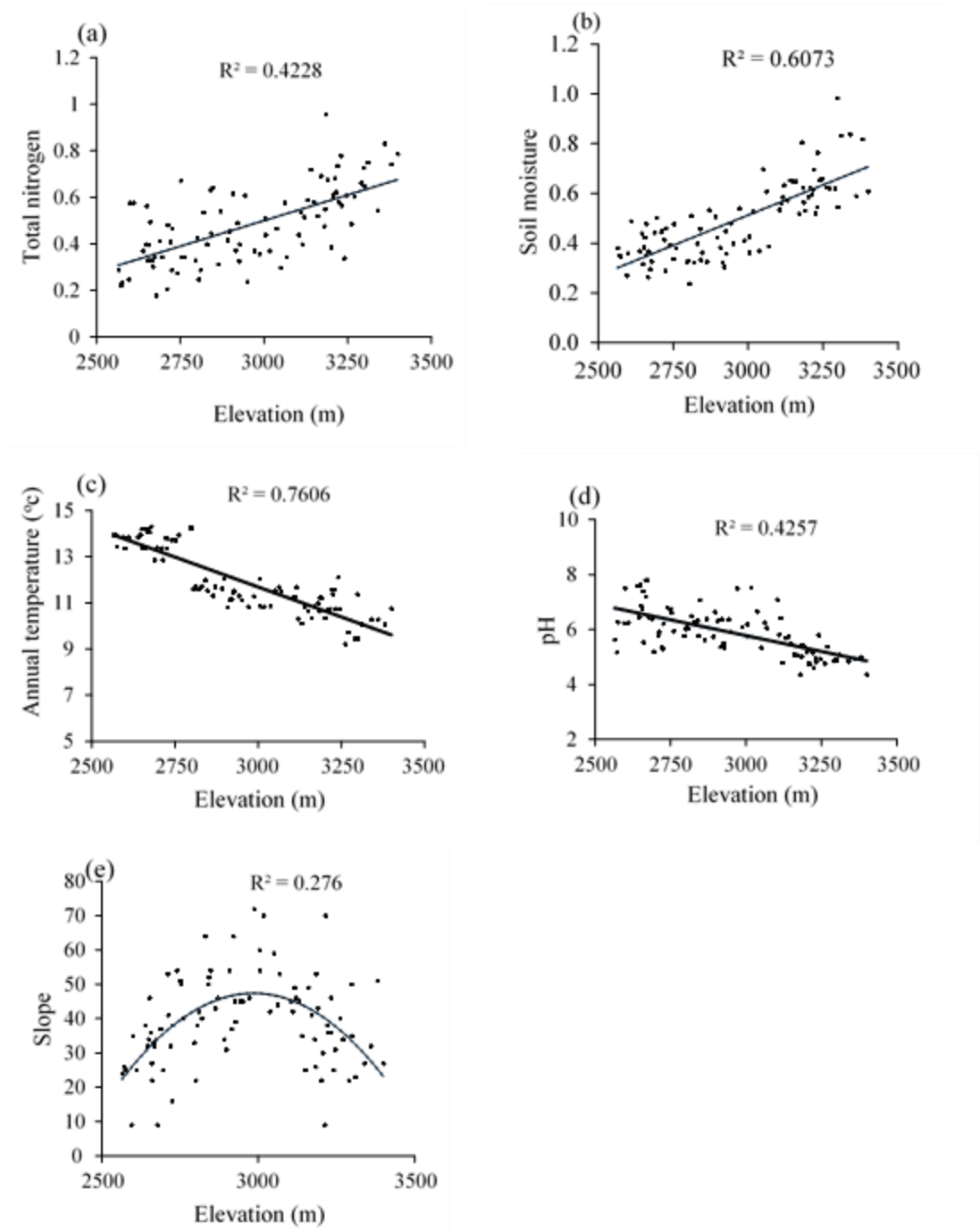


Figure 42. Relationship of elevation with (a) total nitrogen (b) soil moisture (c) annual temperature (d) pH and (e) slope

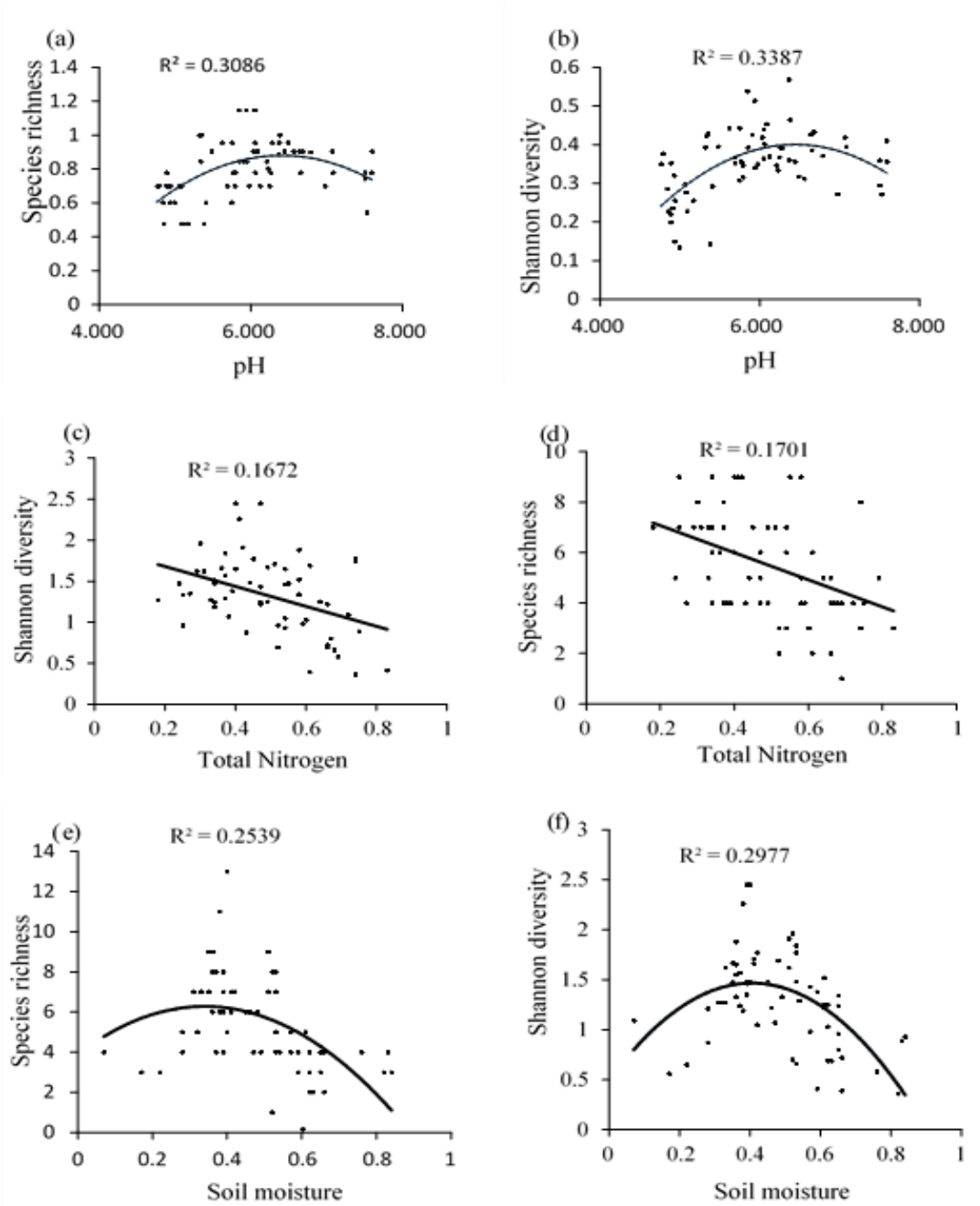


Figure 43. Relationship of species richness and diversity with (a & b) pH, (c & d) TN and (e & f) soil moisture

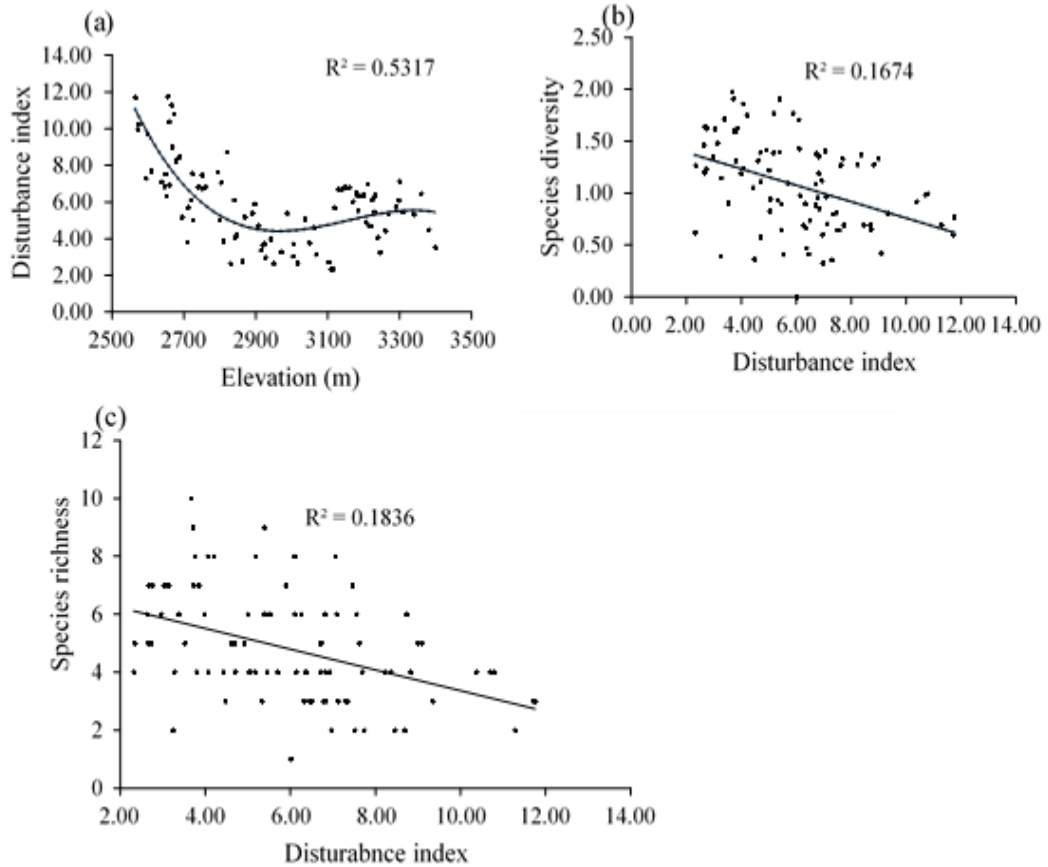


Figure 46. (a) Disturbance index along elevation gradient and (b) species diversity and (c) species richness relationships with disturbance index

4.11.1. Species richness and diversity variation partitioning in entire community

The results of variation partitioning across entire tree species richness and diversity were shown in Table 44. The RDA model constrained the environment and disturbance data was performed to quantify the effects of environmental and disturbance factors on variations in tree species richness and diversity in the entire community. The model showed that environmental and disturbance factors collectively explained 53 % of the richness data and 49 % of the diversity data. Variations in tree species richness with each of the two fractional sets of explanatory variables (environment data and disturbance data) were significant (environment: TVE =37 %; p = 0.045; disturbance: TVE = 24 %; p = 0.045). Similarly, both fractions of environmental and disturbance data sets had significantly (environment: TVE= 19 %; p = 0.005; disturbance: TVE = 26 %; p = 0.005) explained the variations in species diversity in the whole forest community.

The fractional variations explained by the two sets of predictors were partitioned by RDA variance partitioning model and the additive partitioning of variation in tree species richness revealed that a large proportion of variation was explained by pure environmental factor (TVE= 29 %; p = 0.005) than by pure disturbance factor (TVE=16%; p = 0.015). In the whole community along complete elevation gradient, environmental factors explained more variation in species richness than anthropogenic disturbance factors. However, the explained variations by pure environmental and disturbance factors were very close (23% vs 21 %) to each other in case of diversity. This suggested that both environmental and anthropogenic predictors had comparable impact in structuring the patterns of forest diversity in Adaba-Dodola forest in the entire forest community. McIntyre and Lavorel (1994), found similar result in Australia where environmental and disturbance factors are similar in the

extent to which they explained floristic variability in the vegetation.

Elevation exerted significantly the largest portion of variations in species richness (p = 0.005; TVE= 26 %) and diversity (p = 0.005; TVE = 19 %) from the environmental data set, while canopy openness and cutting explained the largest variations in species richness and diversity from the anthropogenic disturbance data set. Elevation was the strongest factors when ranked on the basis of inertia per factor in explaining the variation in species richness and diversity from all components (Table 44). In agreement with this result, McIntyre and Lavorel (1994) revealed that elevation was the dominant factor that controlled diversity and richness for the entire forest along elevation gradient. Because elevation governs a composite gradient of several environmental and climatic variables that act significantly along the changing elevation as an overriding forces (Lomolino, 2001). Soil pH was also important environmental components in explaining the variations of species richness and diversity. Many studies have explored that pH was one of the important plausible driving factors for the prevailing vegetation patterns. Grime (1979) showed the presence of greater number of species in regions with high soil pH. Partel (2002) investigated the positive relationship between species richness and soil pH. However, the prediction of deLafontaine and Houle (2007) was that species richness and diversity should be maximal on low pH sites, which was not supported by our result. Because in our study, the species richness and diversity reached maximum at intermediate (nearly neutral) soil pH sites (about pH 6-7) (Figure 43a & b).

Table 44. Variation partitioning in species richness and diversity for entire communities (Total inertia = 1.00).

Predictor variables	Species richness				Species diversity			
	EV	TVE	*p*	VIF	EV	TVE	*p*	VIF
Environmental variation: [a+b]	0.370	37	0.045		0.27	28	0.005	
Elevation	0.26	26	0.005	3.010	0.19	19	0.005	2.346
Soil moisture	0.02	2	0.190	1.601	0.01	1	0.510	2.478
Slope	0.01	1	0.490	1.237	0.02	2	0.155	1.111
Available P	0.01	1	0.345	2.317	0.01	1	0.620	1.592
Bulk density	0.01	1	0.360	1.353	0.01	1	0.330	1.198
OM	0.01	1	0.450	1.514	0.04	4	0.150	1.373
pH	0.05	5	0.050	3.309				
Disturbance variations: [b+c]	0.238	24	0.045		0.25	26	0.005	
Grazing	0.07	7	0.270	1.011	0.05	5	0.050	1.011
Canopy openness	0.04	4	0.070	1.124	0.01	1	0.580	1.124
Cutting	0.03	3	0.385	1.214	0.17	17	0.005	1.214
Settlement	0.10	10	0.045	1.257	0.03	3	0.100	1.257
Pure environmental variations: [a]	0.292	29	0.005		0.23	23	0.005	
Elevation	0.24	24	0.005	4.842	0.17	17	0.005	3.063
Slope	0.02	2	0.215	1.294	0.02	2	0.205	1.158
Available P				1.902	0.01	1	0.450	1.797
Bulk density				1.696	0.01	1	0.245	1.564
Aspect	0.02	2	0.150	1.322	0.01	1	0.265	1.272
pH	0.01	1	0.350	3.246				
Pure disturbance variation [c]	0.161	16	0.015		0.213	21	0.005	
Canopy openness	0.04	4	0.065	1.393	0	0	0	1.382
Cutting	0.01	1	0.460	1.524	0.13	13	0.010	1.445
Grazing	0.02	2	0.170	1.782				
Settlement	0.10	10	0.015	1.936	0.08	8	0.005	1.842
Total variations: [a+b+c]		53				49		
Shared variation: [b]		8				5		
Residual variation:[100]- [a+b+c]		47				51		

4.11.2. Species richness and diversity variation partitioning in *Podocarpus falcatus-Olea europea* community

Redundancy partitioning of environmental and disturbance influences on species richness and diversity showed that the variations in species richness were

strongly related to the environmental and disturbances descriptors that were included in the study. The RDA forward selection results indicated that environment was the most important factor (Table 45). The environmental and disturbance set jointly explained 75% of the total variations in the species richness of this community. The pure environmental fraction explained 28% (p= 0.005) of the total variations of species richness (Table 45). Our results agreed with many previous studies of Motzkin *et al*. (1999), Svenning and Skov (2002), Gilbert and Lechowicz (2004), Graae *et al*. (2004), and Borchsenius *et al*. (2004), who have shown environment was strong control of landscape and local-scale species distributions and richness.

From environmental variables, elevation was the most environmental factors that strongly explained variations in species richness both when environment was considered as a tandem with disturbance (TVE = 42 %; p = 0.005) and as pure fractions (TVE =13 %; p =0.005) in the *Podocarpus falcatus-Olea europea* forest community.

Pure disturbance fraction had significantly (TVE = 21 %; p = 0.005) explained the variation in the species richness (Table 45). Cutting significantly explained the largest variation (TVE= 36 %; p = 0.005) in species richness in the fraction of disturbances as well as in pure disturbance (TVE = 18 %; p = 0.005). The common share of variance explained by environmental and disturbance predictors [b] was quite high (26%) implying that the two predictors had high confounding effect that were intermingled. Consistent to other mountain areas around the world (Nogue´s-Bravo *et al*., 2008), more forest disturbances took place mainly at low elevation zones of this study area that might be the reason for comparable effect of disturbance with environmental factor in this community. Elevation and cutting were the two most important explanatory variables for tree species richness in this forest community.

The RDA constrained by environmental and disturbance factors to quantify

the effects of the two sets of predictors on variation in tree species diversity indicated that the eigenvalues of the predictors were high indicating that they explained most of the variation in species diversity (Table 46). The joint effect of environment and anthropogenic disturbance factors explained 65% of the total variation in species diversity. Environmental fractions explained 44 % (p = 0.015) of species diversity variations. As a key element of topography, elevation significantly explained 20% *(p* = 0.020) of the variation in the species diversity. Harms *et al.* (2001) and Daws *et al*. (2002) stated that topography is an important driver of habitat diversification that controls spatial variation of hydrological conditions that result in variation of species richness along the topography gradient.

The variation explained by pure environmental factors in species diversity was non-significant when the disturbance effect was extracted by the RDA model (i.e., disturbance factor partialled out). However, pure effect of disturbance was found to be significantly affecting the species diversity still after partialling out of the environmental factors. This showed that variance explaining power of environment in species diversity was enhanced by disturbance factors. The non-significant impact of pure environmental factor might demonstrate that environmental factors were not solely explaining species diversity in *Podocarpus falcatus-Olea europea* vegetation community. In connection with this, Marini *et al.* (2009) explored that the determinants of plant species richness, diversity and composition are most often mutually related, showing that the joint effects on plant species diversity and richness of the plant.

From the disturbance data set, cutting was the most disturbance factor explaining the largest proportion of variation in species diversity both when the covariate was excluded (TVE= 18 %; p = 0.025) or not (TVE= 23%; p = 0.005).

Eleanor *et al*. (2016) stated similar result that there is a quadratic relationship between tree species richness and the number of cut stumps in Tanzania. Alelign *et al*. (2011) on the other hand pointed out that tree cutting affects micro-sites for plant establishment which as a consequence results in the decrease of tree species diversity. Consistent with the current finding, Fadiman (2008) reported that species diversity was decreasing when the preferred tree species are removed by cutting. The study result of Bhattarai *et al.* (2004) on Himalayan elevational gradient reported that the small number of species (low richness) found in the forest might be a result of habitat loss due to deforestation.

In general, disturbance had significantly explained more variation in species diversity as a pure effect in *Podocarpus falcatus-Olea europea* vegetation community. This could be also confirmed by very small variation shared by the two data sets [b] (TVE= 5 %) showing that the joint effect of the two sets of predictors was very minimal and hence the role of environment was insignificant.

Table 45. Variance partitioning in species richness in *Podocarpus falcatus-Olea europea* forest community

Predictor variables	Eigenvalue	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.543	54	0.005	
Elevation	0.42	42	0.005	2.15
Slope	0.06	6	0.095	2.04
Total nitrogen	0.02	2	0.305	2.24
Soil moisture	0.01	1	0.410	1.36
Available P	0.01	1	0.4750	2.59
OM	0.01	1	0.600	1.89
Disturbance variations: [b+c]	0.473	47	0.005	
Canopy openness	0.36	36	0.005	1.18
Settlement	0.07	7	0.115	1.74
Grazing	0.03	3	0.260	1.17
Cutting	0.01	1	0.590	
Pure environmental variations: [a]	0.282	28	0.005	
Elevation	0.13	13	0.005	4.66
Available P	0.06	6	0.095	3.86
Slope	0.03	3	0.130	1.95
Total nitrogen	0.02	2	0.260	3.31
Soil moisture	0.02	2	0.320	2.18
Aspect	0.01	1	0.440	1.99
Electrical conductivity	0.01	1	0.750	7.32
Pure disturbance variation: [c]	0.213	21	0.005	
Cutting	0.18	18	0.005	2.44
Grazing	0.02	2	0.260	2.21
Settlement	0.01	1	0.490	5.72
Total variations: [a+b+c]		75		
Shared variation: [b]		26		
Residual fraction of variation [100]- [a+b+c]		23		

TVE= Total variance explained; VIF= variance inflation factor

Table 46. Variance partitioning in tree species diversity in *Podocarpus falcatus-Olea europea* forest community

Predictor variables	Eigenvalue	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.442	44	0.015	
Elevation	0.20	20	0.020	2.16
Available P	0.06	6	0.205	3.09
Soil moisture	0.05	5	0.215	1.48
Slope	0.03	3	0.345	2.32
OM	0.03	3	0.335	1.89
pH	0.02	2	0.465	3.68
EC	0.02	2	0.420	6.79
Total nitrogen	0.01	1	0.620	2.99
Aspect	0.01	1	0.655	1.43
Bulk density	0.01	1	0.580	1.89
Disturbance variations: [b+c]	0.255	26	0.015	
Cutting	0.23	23	0.025	3.25
Settlement	0.02	2	0.415	1.10
Grazing	0.01	1	0.845	1.01
Pure environmental variations: [a]	0.389	39	0.090	
OM	0.10	10	0.090	3.63
Bulk density	0.6	6	0.180	1.94
Aspect	0.07	7	0.235	2.19
Total nitrogen	0.04	4	0.235	3.31
Soil moisture	0.03	3	0.285	2.12
Slope	0.03	3	0.365	1.85
pH	0.03	3	0.360	4.38
EC	0.03	3	0.430	7.19
Elevation	0.01	1	0.740	4.71
Pure disturbance variation: [c]	0.213	21	0.005	
Cutting	0.18	18	0.005	3.38
Grazing	0.02	2	0.260	2.21
Settlement	0.01	1	0.490	5.72
Environment and disturbance variations		65		
Shared variation: [b]		5		
Residual fraction of variation [100]- [a+b+c]		35		

TVE= Total variance explained; VIF= variance inflation factor

4.11.3. Species richness and diversity variation partitioning in *Juniperus procera-Galiniera saxifraga* community

This forest community was characterized with intermediate levels of environmental factors (e.g. soil pH, soil moisture, soil total nitrogen, etc.) and relatively low disturbance factors (e.g. cutting, settlement, grazing). Significantly, the highest plant species richness and diversity were recorded in this community. This might be attributed to the moderate disturbance and climatic factors of the site. The RDA analytical model detected that the variations of species richness and diversity were related to environmental and disturbance factors. These predictors jointly explained 72 % and 70 % variations in species richness and diversity, respectively (Table 47). The variations explained by environmental factors were significant both in species richness (TVE = 58 %, p = 0.010) and diversity (TVE = 51 %; p = 0.05). However, disturbance factors did not explain significant variations both in species richness (TVE =19 %; p = 0.115) and diversity (TVE = 24 %; p = 0.135).

The non-significant effect of disturbance in the middle part of the gradient was probably related to the low effect of anthropogenic disturbances (cutting, grazing/ browsing and human settlement) in this site. The ANOVA analysis of the disturbance variables of this community also confirmed that there was relatively low proximity (large distance) of human settlement to forest, low stump number (number of trees cut) and low grazing/browsing records of the area. Moreover, there was also high topographic roughness (steep & undulating slope) in this community site that might have also hindered the ease anthropogenic activities in the form of agriculture, deforestation, settlement and animal grazing/ browsing. Marini *et al.* (2011) reported similar result that topographic roughness limits the accessibility to human deforestation and animal entry into the forest that might result in poor species richness

and diversity. According to Marini *et al.* (2010), the middle gradient where the climate is supposed to be optimal, the environmental factors were the most predictors explaining the variation in species richness and diversity.

Secondly, there were also optimum records of soil pH, soil moisture and soil total nitrogen in this vegetation community which might have favored for the increase of species richness and diversity in this site. Plants cannot tolerate either too low or too high pH whereby in very high or low pH habitats, species richness may be reduced (Liu *et al.* 2012). In this study, we found the lowest values of species richness and diversity at the two extreme elevation zones, the upper and lowest elevation zones, where pH was lowest and highest, respectively. Some of the high land species associated with low pH include *Erica arborea*, *Hypercum revolutum*, *Hagenia abyssinica*, etc. while some species associated with high pH include *podocarpus falcatus, Ekebergia capensis, Bersama abyssinica, Carissa spinarum,* etc.

Table 47. Variance partitioning in tree species richness in *Juniperus procera-Galiniera saxifraga* vegetation

Predictors	Eigenvalue	TVE (%)	p-value	VIF
Environmental variation [a+b]	0.584	58	0.015	
Elevation	0.42	42	0.015	2.72
Soil moisture	0.06	6	0.045	2.50
pH	0.05	5	0.045	2.03
OM	0.03	3	0.630	2.41
Total nitrogen	0.02	2	0.575	1.39
Disturbance variations [b+c]	0.19	19	0.115	
Cutting	0.14	14	0.160	2.25
Settlement	0.03	3	0.580	1.36
Grazing	0.01	1	0.850	1.80
Canopy openness	0.01	1	0.820	2.55
Pure environmental variations: [a]	0.531	53	0.045	
Elevation	0.31	31	0.045	2.77
Soil moisture	0.18	18	0.045	3.75
OM	0.01	1	0.755	2.31
Total nitrogen	0.03	3	0.540	2.16
Pure disturbance variation: [c]	0.144	14	0.095	
Cutting	0.09	9	0.090	4.21
Grazing	0.03	3	0.465	2.63
Settlement	0.03	3	0.510	2.41
Canopy openness	0.01	1	0.860	4.29
Envt and disturbance variations: [a+b+c]		72		
Shared variation: [b]		5		
Residual variation: [100]- [a+b+c]		28		

TVE= Total variance explained; VIF= variance inflation factor

Table 48. Variance partitioning in tree species diversity in *Juniperus procera-Galiniera saxifraga* vegetation community

Predictors	Eigenvalue	TVE (%)	*p*-value	VIF
Environmental variation:[a+b]	0.51	51	0.050	
Elevation	0.16	16	0.090	2.50
OM	0.09	9	0.050	2.52
Aspect	0.09	9	0.310	1.56
Moisture content	0.07	7	0.460	2.60
Electric conductivity	0.06	6	0.505	1.65
Total nitrogen	0.04	4	0.455	1.39
Disturbance variations:[b+c]	0.241	24	0.135	
Cutting	0.19	19	0.135	2.25
Settlement	0.02	2	0.680	1.36
Canopy openness	0.03	3	0.610	2.55
Grazing	0.00	0	0.895	1.80
Pure environmental variations: [a]	0.459	46	0.025	
Elevation	0.28	28	0.045	2.87
OM	0.13	13	0.030	2.95
Moisture content	0.04	4	0.410	3.78
Aspect	0.01	1	0.200	5.68
Total nitrogen	0.00	0	1.00	2.55
Pure disturbance variation: [c]	0.19	19	0.115	
Canopy openness	0.10	10	0.185	2.03
Grazing	0.08	8	0.185	5.87
Cutting	0.01	1	0.258	3.97
Settlement	0.01	1	1.00	2.20
Envt and disturbance variations: [a+b+c]		70		
Shared variation: [b]		5		
Residual fraction of variation: [100]- [a+b+c]		30		

4.11.4. Species richness and diversity variance partitioning in *Myrsine melanophloeos - Hagenia abyssinica* community

Species richness and diversity at different clusters respond differently to environmental and human disturbance factors in most cases. This implied that different clustered communities had distinct environmental requirements and respond differently to human disturbance and environmental factors. Some environmental variables explain the variation in species diversity and species richness differently, i.e., the same variables had different explaining power of variations in two different response variables.

In RDA variation partitioning analysis, the environmental factors had significant effect on the variation of the species richness and diversity (Table 49). However, disturbance factors did not explain significant variation in both species richness and diversity. The declined species richness and diversity at high elevation zone of this study might be related to the low energy (low temperature) constraint at the upper elevation, which in turn might have brought about slow regeneration of plants (Bhattarai *et al*., 2004). In agreement with this study, Marini *et al.* (2010) found that at the upper elevational zones, the influence of climatic and climatic related factors (climatic is highly limited by elevation) play a great role in shaping the vegetation structure.

After partialling out the covariance from each set of predictor (environment and disturbance), pure disturbance [c] and pure environment [a] fractions explained significant variations in species richness (disturbance: TVE= 9 %; p = 0.005; environment: TVE = 36 %; p = 0.045) (Table 49). Animal grazing/ browsing (TVE= 16 %; p = 0.010) and elevation (TVE= 33 %; p = 0.045) negatively and significantly influenced the diversity when the covariates were partialled out in the community. The

common share of variation explained by environmental and disturbance predictors [b] was 17 % in richness and 29 % in diversity (Table 50).

Table 49. Variance partitioning in species richness in *Myrsine melanophloeos-Hagenia abyssinica* vegetation community

Predictors	Eigenvalue	TVE (%)	*p*-value	VIF
Environmental variation [a+b]	0.53	53	0.010	
Elevation	0.50	50	0.010	1.07
Slope	0.01	1	0.610	1.15
Bulk density	0.02	2	0.590	1.08
Disturbance variations [b+c]	0.26	26	0.065	
Settlement (habitation	0.10	10	0.080	2.07
Grazing/browsing	0.08	8	0.390	1.04
Cutting (stump density)	0.08	8	0.330	1.37
Pure environmental variations: [a]	0.362	36	0.045	
Elevation	0.36	36	0.045	6.66
Pure disturbance variation: [c]	0.09	9	0.005	
Grazing	0.07	7	0.005	3.93
Settlement	0.01	1	0.200	5.52
Cutting	0.01	1	0.095	2.78
Envt and disturbance variations: [a+b+c]		62		
Shared variation: [b]		17		
Residual variation:[d]= [100]- [a+b+c]		38		

TVE= Total variance explained; VIF= variance inflation factor

Table 50. Variance partitioning in species diversity in *Myrsine melanophloeos-Hagenia abyssinica* community

Predictors	Eigenvalue	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.62	62	0.010	
Elevation	0.50	50	0.010	1.71
Slope	0.07	7	0.325	1.43
Bulk density	0.02	2	0.485	2.23
Aspect	0.03	3	0.540	1.98
Disturbance variations: [b+c]	0.459	46	0.115	
Settlement	0.17	17	0.115	2.07
Grazing	0.15	15	0.230	1.04
Cutting	0.14	14	0.280	1.37
Pure environmental variations: [a]	0.33	33	0.045	
Elevation	0.33	33	0.045	4.27
Pure disturbance variation: [c]	0.172	17	0.010	
Grazing	0.16	16	0.010	1.77
Cutting	0.01	1	0.645	2.29
Envt and disturbance variations: [a+b+c]		79		
Shared variation: [b]		29		
Residual fraction of variation: [100]- [a+b+c]		21		

TVE= Total variance explained; VIF= variance inflation factor

4.11.5. Species richness and diversity variance partitioning in *Erica arborea-Hypercum revolutum* Community

A total of 65 % and 85 % of variation in species richness and diversity, respectively were accounted for by environmental and disturbance predictors in *Erica arborea- Hypercum revolutum* community. The environmental and disturbance factors accounted for 58 % (p= 0.015) and 33% (p= 0.015) variations in species richness and 58 % (p= 0.005*)* and 37% (p= 0.015*)* variations in species diversity, respectively. The unique variations explained by environment and disturbance predictors were 32 % (p = 0.150) and 7% (p = 0.310) in species richness and 48% (p= 0.005) and 27% (p= 0.056) in species diversity, respectively. The non-partialled environmental factors explained equal amount of variations (58 %) both in species richness and diversity.

When the individual environmental variables decomposed, soil pH accounted negatively and significantly for the largest percentage of variation in species richness (p = 0.020; TVE=28 %). This result was in accordance with Benayas *et al*. (2002) and Partel (2002) who reported that the species richness declined in acidic soil. Grime (1979) observed a positive relationship between species richness and soil pH. However, the prediction of deLafontaine and Houle (2007) was that species richness should be maximal on low pH sites that were not supported by our result. Our result showed similarity with Grime (1979) where species richness increased with increasing soil pH until reaching a peak at pH level of about 6-7 and then progressively declined.

There was high total nitrogen in this community that might be resulted from slow OM decomposition (mineralization) due to low temperature. Similarly, Zhang *et al*. (2010) reported soil TN increased with increasing altitude probably due to the lower soil temperatures that would retard the decomposition rate of litters. Ji (1996) also reported lower soil temperatures results in the accumulation of TN in the soils.

Total nitrogen (TN) explained significant variations in species diversity in this community (p = 0.005; TVE= 39 %). The total nitrogen in this study area, particularly at higher elevation, was negatively related to both species richness and diversity. When the species diversity was regressed against total nitrogen, the species diversity started to decline in this community, especially after about 0.4 % of total nitrogen. The current finding was confirmed by the previous studies of Richard *et al*. (2015) who investigated the negative effect of high total nitrogen on species richness and diversity. Previous study of Pausas and Austin (2001), found the unimodal response of species diversity and richness to total nitrogen. Dupré and Diekmann (2002), Hofmeister *et al* (2009) and Jones and Chapman (2011) most often identified the negative trend of species diversity and richness with total nitrogen in temperate deciduous forests. Jones

and Chapman (2011) found also a negative decreasing trend of species richness and diversity in Pennsylvania oak forests. According to Hofmeister *et al.* (2009), the negative effect of total soil nitrogen content on species diversity was due to positive effect of nitrogen on certain highly competitive plants and suppresses the less competent species. In our study site, the nitrogen-rich sites were dominated by species such as *Erica arborea, Hypercum revolutum, Hagenia abyssinca, Discopodium pelllnervium, Mersine melanophleos* and *Nuxia congesta*.

Canopy openness explained significantly the largest proportion of variation in species richness (p= 0.005; VE= 26%) of this community. Mulugeta *et al*. (2004) reported that open canopies could enhance woody species richness than stands with closed canopies. They stated that openings in the forest canopy are widely recognized as important for the establishment and growth of seedlings. Hartshorn (1978) suggests that about 75 % of the tree species are dependent on canopy opening for seed germination or for growth beyond sapling size in Costa Rica. Cayuela *et al*. (2006) explained that moderate canopy openness favors the species richness because it develops favorable environmental conditions especially the availability of light and moisture. The pure effect of both environmental and disturbance predictors had no significant impact on species richness variation in this particular community (Table 51).

Table 51. Variance partitioning in species richness in *Erica arborea-Hypercum revolutum* community (TI=1)

Predictors	Eigenvalue	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.580	58	0.015	
pH	0.28	28	0.020	2.50
Slope	0.08	8	0.155	2.23
Available P	0.07	7	0.175	2.30
Elevation	0.04	4	0.370	3.48
Bulk density	0.04	4	0.320	2.42
EC	0.04	4	0.280	1.95
Total nitrogen	0.02	2	0.460	2.46
OM	0.01	1	0.615	2.01
Disturbance variations: [b+c]	0.333	33	0.015	
Canopy openness	0.26	26	0.015	1.15
Settlement	0.05	5	0.260	1.24
Cutting	0.02	2	0.615	1.05
Pure environmental variations: [a]	0.318	32	0.150	
pH	0.09	9	0.180	3.22
Slope	0.05	5	0.285	3.16
EC	0.05	5	0.305	2.67
Bulk density	0.05	5	0.285	2.99
Elevation	0.03	3	0.400	3.21
Aspect	0.03	3	0.435	1.62
AvP	0.02	2	0.485	2.73
Pure disturbance variation: [c]	0.071	7	0.310	
Grazing	0.05	5	0.310	2.08
Cutting	0.02	2	0.580	2.70
Envt and disturbance variations: [a+b+c]		65		
Shared variation: [b]		26		
Residual fraction of variation: 100- [a+b+c]		35		

Table 52. Variance partitioning in tree species diversity in *Erica arborea-Hypercum revolutum* community

Predictors	Eigenvalue	TVE (%)	*p*-value	VIF
Environmental variation: [a+b]	0.584	58	0.005	
Total nitrogen	0.39	39	0.005	2.69
Elevation	0.11	11	0.050	4.04
pH	0.03	3	0.310	2.22
Aspect	0.02	2	0.395	1.48
EC	0.02	2	0.410	1.74
Bulk density	0.01	1	0.645	2.19
Disturbance variations: [b+c]	0.368	37	0.015	
Canopy openness	0.12	12	0.115	1.12
Settlement (habitation)	0.10	10	0.190	1.13
Cutting (stump density)	0.15	15	0.090	1.03
Pure environmental variations: [a]	0.480	48	0.005	
Total nitrogen	0.32	32	0.005	4.58
pH	0.05	5	0.045	4.60
EC	0.04	4	0.245	3.37
Elevation	0.02	2	0.325	6.70
Aspect	0.02	2	0.295	3.44
Slope	0.01	1	0.430	3.71
AvP	0.01	1	0.595	2.83
Pure disturbance variation: [c]	0.274	27	0.056	
Settlement	0.14	14	0.070	4.63
Grazing	0.07	7	0.140	2.08
Cutting	0.05	5	0.165	2.70
Canopy openness	0.01	1	0.545	2.91
Envt and disturbance variations [a+b+c]		85		
Shared variation: [b]		10		
Residual fraction of variation: 100- [a+b+c]		15		

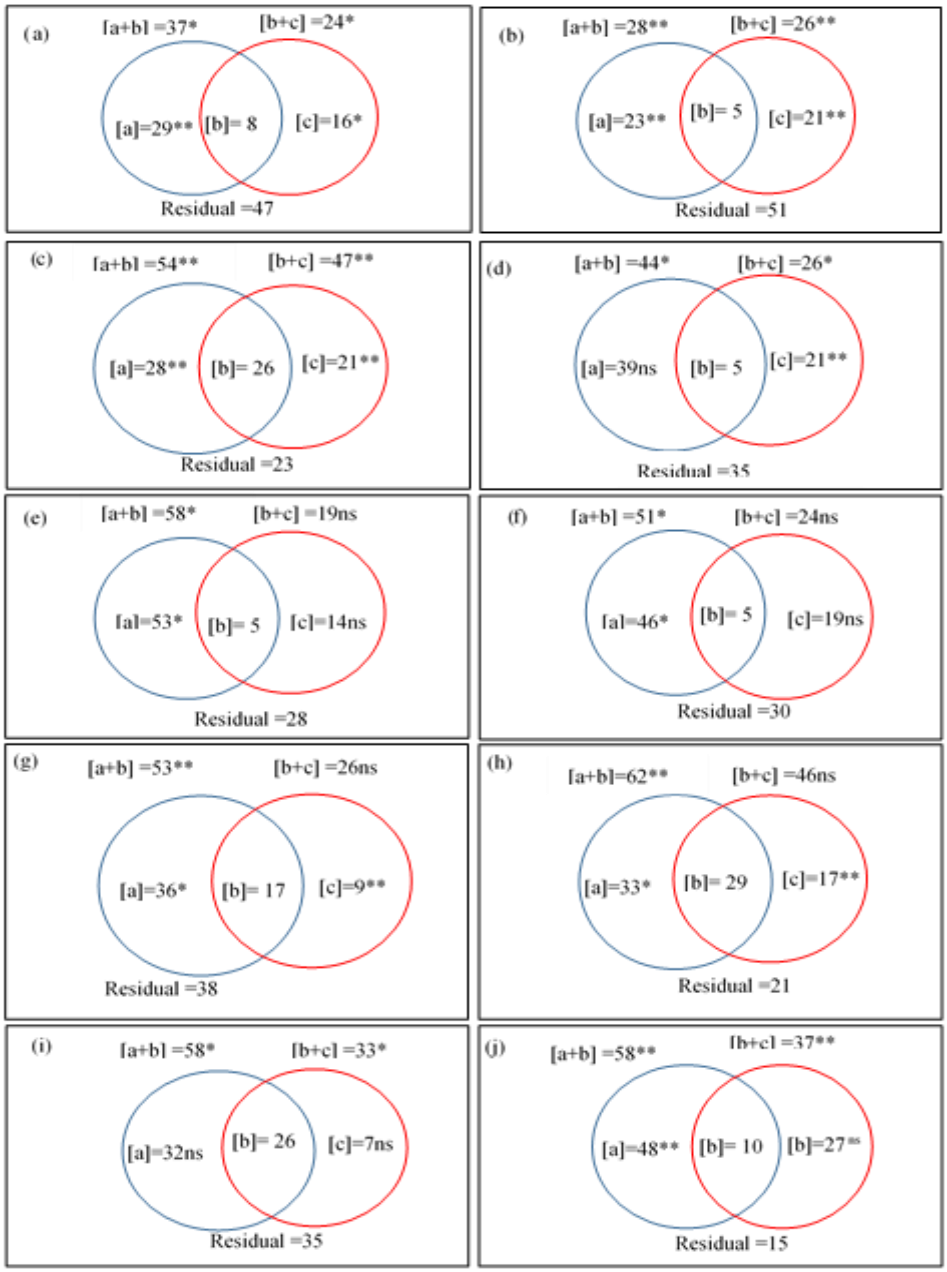


Figure 47. Summary of variance partitioning Venn diagram

Variance partitioning Venn diagram for :(a) species richness in whole community (b) species diversity in whole community (c) species richness in community I (d) species diversity in community I (e) species richness in community II (f) species diversity community II (g) species richness in community III (h) species diversity in community III (i) species richness in community IV (j) species diversity in community IV. [a+b] = environmental fraction; [b+c] = disturbance fraction; [a] = pure effect of environment; [b] = shared variation; [c] = pure effect of disturbance. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = non-significant

CONCLUSIONS

This study is the first to explore the relative roles of environmental and anthropogenic disturbance factors in determining forest distribution, composition and diversity in south eastern Ethiopian Afromontane forests. The result of this study is particularly important for conservation and sustainable use of biodiversity in Ethiopia where the wide range of altitudes and high topographic variability gives rise to high species diversity.

In developing country like Ethiopia where there is high competition between agriculture and forest development, it is exceptionally difficult to reserve large areas of land for biodiversity conservation. Therefore, the present study investigated the species rich and species rare zones and the major drivers for the change of vegetation patterns which can help prioritize sites for biodiversity conservation. The multivariate analysis by CCA/RDA models indicated that environmental (elevation, slope, aspect and soil edaphic factors) and the anthropogenic factors (cutting, grazing, settlement and canopy openness) were recognized as potential drivers of vegetation patterns.

The results of the present study clearly showed that forest disturbance due to human and environmental factors had significantly affected the Afromontane forests of Adaba-Dodola though they have different effect and influencing power in different communities and elevation zones. The anthropogenic disturbance data set had less effect on variations of the vegetation attributes in mid part of the elevation, in *Juniperus procera-Galiniera saxifrage* forest community, which might be mainly related to the high topographic roughness (sloppy terrain) that limited the accessibility to human and animal influences. Moreover, the middle site was found at transitional zone between the lower and the upper elevational zones that can share some climatic

characteristics with both high and low elevation zones which in turn support the more number of species to coexist.

In the lowlands, favorable topography (flat terrain) for humans and very near human settlements to forest sites mainly triggered the destruction and homogenization of habitats which, in turn, reduced species richness and diversity. Effect of disturbance was found to be the main factor for the decline of species diversity and richness at low elevations while that of the upper end elevation zone were mainly related to environmental factors (edaphic and climatic) rather than the disturbance activities.

Generally, the Adaba-Dodola Afromontane forest was characterized with low species richness, diversity and natural regeneration. The species dominance status evaluated based on ecological dominance analysis, an overall of about 81% of the species in the Adaba-Dodola Afromontane forest require immediate conservation priority. The Jaccard coefficient of similarity analysis also showed a very low similarity between the seed bank and standing vegetation. The soil seed bank germination experiment revealed 68% of the soil seed bank individuals were not representing their own standing vegetation species.

Likewise, the species regeneration potential evaluated based on age group proportion of species indicated that about 75 % of the woody species were categorized as fair, poor and no regeneration. Only few woody species such as *Myrsine melanophloeos, Myrsine africana, Dovyalis abyssinica* and *Bersama abyssinica* had better chances of recovery since they were moderately represented in the soil seed banks. Especially, low elevation and upper elevation forest communities had poor regeneration status. This implies that it is unlikely that seed banks will serve as the only solution for the rehabilitation of the degraded Adaba-Dodola Afromontane forest.

Therefore, enrichment planting with adaptable tree seedlings should be undertaken for successful vegetation restoration in Adaba-Dodola Afromontane forest.

The study clearly revealed that the pattern of species along elevation gradient cannot be attributed to a single universal explanation, rather a combination of many environmental (edaphic and topographic) and anthropogenic factors. Even though, environment was found to be strong control of species distributions, compositions and diversity of forests as general view, it is increasingly important to take anthropogenic effects explicitly into account during vegetation community assessment for conservation planning along elevational gradients. As human activities were intimately connected to the forest ecosystems, the inclusion of anthropogenic-related variables in the present study believed to have explicitly described the potential underlying processes in the pattern of species distribution, richness, composition and diversity and conservation planning in Adaba-Dodola Afromontane forest.

In conclusion, the forest restoration or conservation efforts need to focus on seedling enrichment with quantity (size) and quality (species composition) of species to diversify the species-poor forest sites. Multiple species plantation is also required to restore stable forest functions in addition to biodiversity, particularly in accorardance with the climatic changes. Establishing at least four conservation corridors (protected areas) that incorporate the four identified clustered forest communities in the study is suggested. Considering four corridors for conservation is very important strategy particularly for Adaba-Dodola Afromontane forest due to narrow distribution ranges of most species and high degree of forest fragmentation. During implementation of natural (for species with good regeneration status) and artificial regeneration schemes, animal and human disturbances, especially at seedling establishment and seed production periods should be avoided. Especially, at the mid

and upper altitudes, where *Hagenia* is dominant, a certain portion of the forest areas should be strictly protected from grazing until the young plants are above the reach of the animals.

Based on the current findings, the following points were recommended for future consideration:

- The current study result is based on limited environmental and anthropogenic factors to determined species distribution, composition, richness and diversity patterns. Hence, further investigations on the influence of more environmental (temperature, rainfall, evaporation, transpiration rate, productivity, edaphic) and disturbance factors need to be considered for more comprehensive understanding of the ecosystem.
- The current result is based on single season and single stage data collection. Therefore, undertaking a research on the basis of multistage data collection over seasons and years is recommended.
- The present study depicted that the natural regeneration of tree species in the fragmented forests was generally found to be poor. Thus, supplementary research is required on particularly on the regeneration of indicator tree species identified in each clustered community.
- Further studies on the impact of deforestation and fragmentation on reproductive phenology, seed rain, survival and recruitment of seedlings of tree species exhibiting poor regeneration need to be initiated.
- *In situ* and *ex situ* conservation methods have to be employed for the conservation of species having low importance value index and poor regeneration status
- Practicing the modern agroforestry systems is adivisable to solve the land shortage.

- It is required to encourage tree planting in the homesteads, farmlands hedgerow and churchyards through supply of seedlings of indigenous and appropriate exotic species in order to reduce the pressure on the natural vegetation.
- For the local community to reduce dependency on the natural vegetation for fuelwood, government and non-government organizations should encourage the usage of energy saving stoves.
- To reduce pressure on the natural forests, the government needs to create alternative sources of income and employment opportunities for communities.
- Community awareness creation and training on about sustainable conservation and utilisation of forest is imperative for the successful management of the forests. Moreover, regular discussion forums should be arranged for stakeholders so that they can learn from the past weak relationships and work toward a better way of co-operation and co-ordination.
- Filling the food deficit of the communities in the study area by government can be one of the important options to save the remaining forest.
- Intensive family planning services should be provided to control population growth in study area, which is one of the driving forces in forest degradation.
- Adaba-Dodola Afromontane forest, especially, Bubisa forest site is out of sight of the scientific community primarily due to its lack of accessibility. Due attention should be given to solve the infrastructure problems so that the scientific community can devote more time to look at this poorly known forest for improvement.

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APPENDICES

Appendix 1. Individual number (N) and mean height (H) of species in vertical layers of forest community I

Species	Lower layer		Middle layer		Upper layer	
	N	H (m)	N	H(m)	N	H(m)
Allophyllus abyssinicus	10	7				
Bersama abyssinica	3	4				
Buddleja polystachya	10	6				
Carissa spinarum	9	8				
Dovyalis abyssinica	10	4				
Ekebergia capensis	10	6	4	24		
Galiniera saxifraga	4	6				
Hagenia abyssinica			1	16		
Juniperus procera	246	6	130	23	1	32
Maytenus arbutifolia	5	4				
Maytenus undata	30	6	1	18		
Myrsine Africana	4	4				
Myrsine melanophloeos	23	5				
Nuxia congesta	17	8				
Olea europaea	34	8	2	17		
Olinia rochetiana	11	5	2	20		
Osyris quadripartite	11	5				
Podocarphus falcatus	230	5	64	23	2	45
Prunus africana	1	4	3	25		
Pyschotria orophila	1	6				
Rhamnus staddo	7	5				
Rhus glutjnosa	5	6				
Rosa abyssinica	8	5				
Rubus steudneri	3	6				
Schefflera volkensii	2	7				
Scolopia theifolia	18	5				
Sideroxylon oxyacantbum	1	7				
Vernonia rueppellii	17	4				

Appendix 2. Individual number (N) and mean height (H) of species in vertical layers of forest community II

Species	Lower layer		Middle layer		Upper layer	
	N	H	N	H	N	H
Buddleja polystachya	2	6				
Dombeya torrida	5	7				
Dovyalis abyssinica	2	3				
Ekebergia capensis	8	5				
Erica arborea	4	6				
Galiniera saxifraga	24	6				
Hagenia abyssinica	5	7	9	15	4	24
Hypericum revolutum	4	7				
Inula confertiflora	6	4				
Juniperus procera	77	6	22	15	48	26
Lobelia rhychnchopetalum	1	7				
Maytenus undata	2	7	3	14		
Myrica salicifolia	1	8				
Myrsine Africana	8	3				
Myrsine melanophloeos	25	6			1	25
Nuxia congesta	14	6				
Olea europaea	16	5	3	15		
Olinia rochetiana	2	7	1	10		
Osyris quadripartite	19	4				
Podocarphus falcatus	16	6	4	13	1	22
Prunus africana	1	5				
Rhus glutjnosa	1	7				
Rubus steudneri	1	5				
Schefflera myriantha	1	7				
Schefflera volkensii	4	5	1	15		

Appendix 3. Individual number (N) and mean height (H) of species in vertical layers of forest community III

Species	Lower layer		Middle layer		Upper layer	
	N	H	N	H	N	H
Erica arborea			3	11		
Galiniera saxifraga	2	6				
Hagenia abyssinica			2	17	4	21
Hypericum revolutum	17	5	25	11		
Inula confertiflora	1	4				
Juniperus procera	2	4	9	16	17	24
Maesa lanceolata	1	4				
Maytenus undata	1	7				
Myrsine melanophloeos	52	6	6	11		
Nuxia congesta	1	8				
Osyris quadripartite	1	4				
Podocarphus falcatus	2	4				
Rubus steudneri Schweinf	1	4				
Schefflera volkensii	2	8	2	14		
Vernonia rueppellii	2	5				

Appendix 4. Individual number (N) and mean height (H) of species in vertical layers of forest community IV

Species	Lower layer		Middle layer		Upper layer	
	N	H	N	H	N	H
Buddleja polystachya	1	8				
Discopodium pennlnervium	2	3				
Erica arborea	290	6	139	11	2	25
Gnidia glauca	4	5				
Hagenia abyssinica	2	6	16	16	1	24
Hypericum revolutum	43	7	76	11		
Inula confertiflora	7	3				
Juniperus procera					2	25
Myrsine melanophloeos	34	6	11	11		
Nuxia congesta	4	6				
Olinia rochetiana	1	3				
Osyris quadripartite	2	5				
Schefflera volkensii	5	6	6	13		

Appendix 5. List of woody and herbaceous species recorded in the soil seedbank layers

Species	0-3 cm	3-6 cm	6-9 cm
Grass			
Cynodon dactylon (L.) Pers.	+	+	+
Eleusine floccifolia (Forssk.) Spreng.		+	
Eragrostis paposa (Roem.& Schult.)Steud.	+	+	+
Eragrostis schweinfurthii Chiov.	+	+	+
Pennisetum clandestinum Chiov.	+		
Phaenantheocium koestlinii (Hochst.ex A.Rich.)	+	+	+
Sporobolu pilifenas (Tnn.) Kunth	+	+	
Herb and sedges			
Ajuga integrifolia Buch. Ham. ex D. Don.		+	
Campanula edulis Forssk.	+		
Eurphobia dumalis S. Carter	+	+	
Geranium arabicum Forssk	+	+	+
Leucas martinicensis (Jacq.) R. Br.		+	
Medicago polymorpha L.		+	
Plantago lanceolata L.	+	+	+
Satureja abyssinica (Benth.) Briq.	+	+	
Trifolium burchellianum Ser.	+	+	+
Trifolium quartinianum A. Rich.	+	+	+
Trifolium schimperi A. Rich.		+	
Urtica simensis	+		
Cyperus Pauper Rochat. exA. Rich.	+	+	+
Cyperus sesquiflorus (Torr.) Matif. & KU. k.	+	+	+
Shrub			
Achyranthes aspera L.	+	+	+
Crotalaria pycnostachya Benth.	+		+
Datura stramonium L.		+	
Inula confertiflora A. Rich.	+	+	+
Myrsine africana	+	+	+
Rosa abyssinica	+		
Solanum incanum L.	+		+
Solanum marginatum L.f.	+	+	+
Sparmannia ricinocarpa (Eckl. & Zeyh.) Kuntze	+	+	
Vernonia rueppellii Sch. Bip. ex Walp.	+	+	+
Tree			
Dombeya torida	+	+	+
Hagenia abyssinica	+	+	+
Hypericum revolutum	+	+	+
Juniperus procera	+	+	+
Myrsine melanophloeos (L.) R. Br.		+	+
Podocarpus falcatus	+		
Prunus africana		+	
Tree / Shrub			
Maesa lanceolata Forssk.	+		

ABSTRACT IN KOREAN

아다바-도돌라 Afromontane 숲은 에티오피아에서 생물다양성 최우선 보호 대상 지역 중 하나로 여겨져 온 곳이다. 그럼에도 불구하고, 이 숲은 에티오피아의 Afromontane 숲 중에서 작은 조각의 여러 패치들로 파편화되어 가장 훼손된 상태에 있다. 교란의 영향을 줄이고 교란된 숲을 복원하는 것이 이곳 생태계의 기능을 유지하고 생물다양성을 보존하기 위한 최우선의 과제이다. 본 연구는 교란되지 않은 상태로 남겨진 숲들을 유지하는데 도움이 되는 관련 정보를 제공하기 위해 첫째, 숲의 종 구성, 분포 양상, 종 풍부도, 종 다양성, 구조, 그리고 갱신이 자연 환경과 인위적인 교란의 영향에 따라 어떻게 달라지는지를 살펴보고, 둘째, 상이한 고도 별로 이 두 가지의 설명변수가 지니는 상대적인 중요도를 평가하는 것을 목표로 한다.

연구를 위해 세 곳의 조사지를 선정하였으며, 모든 조사지에서 약 1 km 의 간격을 둔 두 개의 트렌섹트에 고도에 따른 구배를 두어 90 개 (20 × 20 m)의 방형구를 설치하였다. 매토종자의 발아 실험은 온실에서 6 개월 동안 수행하였다. 식생과 설명변수들 간의 관계를 고찰하기 위해 정준상관분석 (Canonical Correspondence Analysis, CCA)과 중복분석(Redundancy Analysis, RDA)을 실시하였으며, 종다양성지수를 사용하여 종 다양성, 종 풍부도, 그리고 종 균등도의 경향을 분석하였다. 설명변수들 간의 변량 분할을 위해 CANOCO 프로그램을 이용한 CCA/RDA 분석과 단계적 다중회귀모형을 이용하였고, 주요 독립변수들 간의 평균치검정을 위해 분산분석(ANOVA)을 실시하였다.

CCA/RDA 분석을 통해 도출된 종-환경 서열은 목본 식물 군락들 간의 차이가 환경 요인과 교란 요인에 의해서 설명될 수 있다는 것을 나타낸다. 전체 식생에서 자연 환경과 인위적인 교란의 데이터 세트는 각각 종 다양성의 19 % (p = 0.005)와 26 % (p = 0.005)를 설명하고, 종 풍부도의 37 % (p =

0.045)와 24 % (p < 0.045)를 설명한다. 종 풍부도(R^2 = 0.36; p < 0.006)와 종 다양성(R^2 = 0.47; p < 0.001)은 중간 고도 지역에서 단봉형 모양을 나타내며 현저한 변화를 보였다. 이러한 중간 고도에서의 최대 종 풍부도와 종 다양성은 다변량모형과 분산분석에서 나타났던 여러 요인들에서 기인한 것으로 추정된다. 주요한 원인들 중 하나는 낮은 고도와 높은 고도의 지역에 비해 벌채, 방목, 정착, 수관 소개와 같은 인위적인 활동들이 적었기 때문일 것이다. 낮은 수준의 인위적 교란은 해당 숲 군락의 가파르고 굴곡이 심한 경사와 같이 지형적으로 험준한 특성 때문에 인위적 활동을 위한 사람들의 숲으로의 용이한 접근을 제한해왔던 데에 원인이 있다. 나아가, 중간 고도 지역은 낮은 고도 지역과 높은 고도 지역의 점이지대로써, 두 지역의 특정 기후적 특징을 공유하는 것을 가능하게 했을 것이다. 기후 데이터에 따르면, 이 지역은 중간 정도의 기후 조건(연평균 강우량 1059 mm 와 연평균 기온 11℃)을 가지는 것으로 추정되는데 이러한 환경이 더 많은 수의 식물들로 하여금 서로 공존하도록 하는 데에 유리하게 작용하였을 것이다.

낮은 고도 지역에서는, 순수한 인위적 요인이 그곳의 종 다양성에 유의한 효과(p < 0.005)를 가져온 반면, 순수한 환경적 요인은 유의한 효과를 가져다 주지 못했음을 변량 분할 모형을 통해 확인하였다. 특히, 벌채로 인한 교란이 낮은 고도 지역의 종 다양성에 가장 현저한 효과를 가져다 주었다. 반면, 다변량분석 결과 가장 고도가 높은 지역에서는 순수한 환경적 요인이 이 지역의 종 다양성 감소에 중요한 영향을 미친 것으로 나타났는데, 이는 이 지역의 종 다양성 감소가 주로 인위적 교란보다는 환경적 요인 때문이라는 것을 암시한다. 또한, 높은 전질소 수치가 높은 고도 지역의 종 다양성과 종 풍부도에 부정적인 영향을 미쳤다. 이러한 결과는 높은 질소 함량이 고도의 경쟁력을 보이는 특정 식물들로 하여금 경쟁력이 낮은 식물들을 약화시키고, 억누르고, 배제시키는 데에 정의 효과를 가져다 주었고, 이것이 곧 종 다양성의

감소로 이어졌기 때문인 것으로 설명할 수 있을 것이다. 나아가, 높은 고도 지역의 낮은 기온(연평균 기온 1.7℃)이 식물들의 생장과 갱신의 속도를 늦춤으로써 종 풍부도와 종 다양성을 감소시킨 이유였을 것으로 추정된다.

매토종자에서 보이는 종 다양성에 있어서의 커다란 차이는 벌채(R^2adj =10.8 %; p = 0.038), 토양 pH(R^2adj = 5.1%; p= 0.029), 그리고 향(R^2adj = 5.0%; p = 0.014) 순으로 설명력을 갖는 것으로 나타났다. Jaccard 계수에 따르면, 현존 식생과 매토종자 사이에는 73%의 비유사성이 있었다. 이러한 불일치 문제의 원인에는 여러 가지가 있을 수 있다. 이는 땅속에서 살아남기 위해 필요한 휴면 기작이 결여되어 활성이 오래 유지되지 못하는 매토종자, 또는, 조기 발아를 막는 내과피 휴면(예, *Juniperus procera* 와 *Olea europaea*), 또는, 포식자를 유인하는 과육질의 열매로 인한 동물(곤충)에 의한 높은 섭식 비율(예, *Juniperus procera, Ekebergia carpesis*, 그리고, *Podocarpus falcatus* 의 종자), 또는, 진균성 토양감염질병으로 인한 낮은 생존율(예, *Podocarpus falcatus*; 최근의 *Podocarpus falcatus* 종자의 생존율에 관한 연구에 따르면 2.1%를 나타냄) 때문으로 볼 수 있다. 매토종자 실험에 의하면, 지상부 식생 중 목본 식물의 약 68%가 매토종자로부터 기원하지 않았다. 갱신 단계 분석에 따르면, 아다바-도돌라 Afromontane 숲의 총 종 중 약 41.27%는 전혀 갱신을 하지 않았고, 25.40%는 상당한 수준의 갱신을 진행하고 있었으며, 그리고 9.52%는 낮은 수준의 갱신 상태를 보였다. 나아가, 우점도 분석 또한 목본 식물의 약 81%가 즉각적으로 우선적인 보호 조치가 필요한 것으로 나타났다.

본 연구에서의 중요한 발견은 인위적인 교란과 환경 요인들의 집합적인 효과가 지상부 식생과 매토종자 모두에서 종의 분포와 종 풍부도, 그리고 종 다양성의 고도에 따른 전반적인 경향을 구체화하는 가능성 있는 기작을 설명했다는 데에 있다. 교란의 효과, 특히, 벌채는 낮은 고도 지역에서

종 다양성의 감소를 야기한 주요한 요인인 것으로 확인된 반면, 가장 고도가 높은 지역에서 종 다양성을 감소시킨 원인은 인간의 교란 활동이 아니라 주로 환경 요인들과 관련이 있었다. 이것은 관찰된 식생 양상들이 하나의 보편적인 이유보다는 환경과 인위적 요인들의 조합 때문이라는 것을 암시한다. 그러므로, 고도의 변화에 따른 생태적 경과를 기술할 때에는 인위적인 효과들을 고려하는 것이 매우 중요하다.

종합적인 결론으로, 새로운 환경에 적응할 수 있는 실생묘를 심어 종 구성의 다양성을 높이는 것이 성공적인 식생 복원을 위해, 특히, 중요치가 낮고 갱신 수준이 낮은 식물들에 요구되는 상황에서, 오직 천연 갱신에만 의존하는 것은 훼손된 아다바-도돌라 Afromontane 숲의 복원을 위한 효과적인 전략이 아닐 수도 있다. 숲 복원이나 보전 노력은 양적 수준뿐만 아니라 종 구성이 빈약한 지역에 종 다양성을 높이는 질적 수준을 함께 유지해나가는 데에 초점을 맞출 필요가 있다. 방목과 경작으로 인한 교란을 경감하는 것은 본 연구지의 숲 보전 계획 수립을 위해 고려할 수 있는 주요 조치들 중 하나가 되어야 한다.

주요어: Afromontane 숲, 다양성, 고도, 갱신, 매토종자, 종 풍부도